Canadian Journal of Fisheries and Aquatic Sciences
 Journal canadien des sciences halieutiques et aquatiques

**Fine-scale movement of juvenile Atlantic sturgeon
 (*Acipenser oxyrinchus oxyrinchus*) during aggregations in
 the lower Saint John River Basin, New Brunswick, Canada**

Journal:	<i>Canadian Journal of Fisheries and Aquatic Sciences</i>
Manuscript ID	cjfas-2017-0430.R1
Manuscript Type:	Article
Date Submitted by the Author:	12-Jan-2018
Complete List of Authors:	Whitmore, Margaret; Mount Allison University, Department of Biology Litvak, Matthew; Mount Allison University, Department of Biology
Is the invited manuscript for consideration in a Special Issue? :	Oceans Tracking Network
Keyword:	Acoustic telemetry, Vemco Positioning System, T-LoCoH, Aggregation behavior, Space use

SCHOLARONE™
 Manuscripts

January 12, 2018

Fine-scale movement of juvenile Atlantic sturgeon (*Acipenser oxyrinchus oxyrinchus*) during aggregations in the lower Saint John River Basin, New Brunswick, Canada

Margaret M. Whitmore¹, Matthew K. Litvak¹

Keywords: Acoustic telemetry, Vemco Positioning System, movement ecology, T-LoCoH, space use, aggregation behavior

¹ Mount Allison University
Department of Biology
62 York Street
Sackville, New Brunswick E4L 1E2
ML: mlitvak@mta.ca
MW: margi.whitmore@gmail.com

Corresponding author:
Margaret M. Whitmore
margi.whitmore@gmail.com
tel: (716) 990-0494

Abstract

Juvenile Atlantic sturgeon form seasonal aggregations near the salt wedge in their natal river systems. We used an array of Vemco Positioning System acoustic receivers to track fine-scale movement within aggregation sites in two rivers in the Saint John River Basin. We used the t-LoCoH convex hull construction algorithm to map space use and aggregation behavior; and nonmetric multidimensional scaling to test for differences between rivers, seasons, and photoperiods. Aggregation sites consisted of small core areas, where juvenile Atlantic sturgeon remained for long periods, that are adjacent to foraging grounds. This structure was largely consistent between rivers and seasons. Directional movement within aggregation sites differed between rivers. In areas of high flow velocity, directional movement was parallel to flow and largely restricted to littoral areas, whereas areas of low flow exhibited no distinct patterns in directional movement. This indicates flow may be an important driver of fine-scale distribution within aggregation sites. Studies of fine-scale space use can inform future investigations of rearing capacity, aid in the identification of critical habitat, and inform management decisions.

60 Introduction

61 Atlantic sturgeon (*Acipenser oxyrinchus oxyrinchus*) are large anadromous fish distributed from
62 Labrador to Florida. Global populations are listed as near threatened by the International Union
63 for the Conservation of Nature (IUCN 2016) and several regional populations are in decline
64 (Patrick and Damon-Randall 2008). Of the five distinct population segments identified in the
65 United States, four are listed as endangered and one as threatened under the Endangered Species
66 Act (NOAA 2012a, 2012b). In Canada, both the St. Lawrence and the Maritimes population
67 units are designated as threatened by the Committee on the Status of Endangered Wildlife in
68 Canada (COSEWIC) and the Maritimes unit is currently being considered for listing as
69 threatened under the Species At Risk Act (SARA) (COSEWIC 2011). The Saint John River in
70 New Brunswick, Canada is one of two active Atlantic sturgeon spawning rivers in Atlantic
71 Canada (Dadswell 2006; Taylor and Litvak 2017). There is a small commercial fishery for
72 Atlantic sturgeon adults in the lower river as well as an active recreational fishery that targets
73 both shortnose (*A. brevirostrum*) and Atlantic sturgeon (DFO 2013).

74 Adult Atlantic sturgeon make extensive movements along the coast (Waldman et al.
75 1996; Erikson et al. 2011) as well as form seasonal aggregations (Dunton et al. 2010; Laney et al.
76 2012; Taylor et al. 2016). Adults have been observed occupying relatively small, core areas
77 within larger home ranges in rivers and coastal waters (Hatin et al. 2002; Wippelhauser et al.
78 2016). Mixed stock aggregations have been identified along the Atlantic coast and in the Bay of
79 Fundy during summer foraging (Dunton et al. 2010; McLean et al. 2013); dense overwintering
80 aggregations in coastal waters (Laney et al. 2007; Taylor et al. 2016); and spawning aggregations
81 in natal rivers in spring and early summer (Hatin et al. 2002).

Investigations of fine-scale space use are scarce and have largely focused on adult and subadult life stages. As a result, relatively little is known about spatiotemporal distribution and aggregation behavior of juveniles, especially at high latitudes. Juveniles appear to exhibit patterns similar to adults, using small core areas within larger home ranges in their natal river systems (Lazzari et al. 1986; Hatin et al. 2002; Hale et al. 2016). Elasticity analysis of Atlantic sturgeon life stages shows survival of early life stages has the highest potential for increasing sturgeon populations (Gross et al. 2002). Identifying aggregation sites and spatiotemporal distribution is crucial in assessing habitat requirements and rearing capacity for a river system as well as for directing sustainable management for the species.

Investigations into Atlantic sturgeon movement reveal a pattern of coarse-scale movements between aggregation areas, where they remain for variable periods of time (Fox et al. 2002; Hatin et al. 2002). We identified a similar pattern in juveniles as part of a larger investigation into their spatiotemporal distribution in the Saint John River Basin (Whitmore, unpublished data). In this study, we focus on these aggregation areas and investigate seasonal patterns of movement and space use at fine-scales using acoustic telemetry. We used a combination of passive and active tracking techniques to identify two aggregation sites in the Saint John and Kennebecasis Rivers and determine approximate boundaries. Fish location is estimated using a Vemco Positioning System (VPS) and t-LoCoH is used to construct home ranges and identify areas of use within aggregation sites. We tested for differences in spatiotemporal distribution between sites, seasons, and photoperiods using nonmetric multidimensional scaling (NMDS) and analysis of similarities (ANOSIM R).

The goals of this study were to identify seasonal and diurnal patterns of space use in aggregation sites and investigate consistency of pattern across sites. During active tracking,

juveniles exhibited periods of station-holding followed by periods of movement suggestive of searching behavior (Whitmore, unpublished data). Previous studies of adult Atlantic sturgeon in the Bay of Fundy suggest adults are more active during dawn and dusk when foraging in intertidal areas (McLean et al. 2014). We hypothesized that 1) juveniles occupy dense core areas within aggregation sites for long durations adjacent to foraging areas and 2) juveniles exhibit higher activity levels during crepuscular periods.

Materials and Methods

Study area

The Saint John River stretches from its headwaters in Maine, through Quebec and New Brunswick, and drains into the Bay of Fundy. The lower Saint John Basin is comprised of two major rivers, the Saint John and Kennebecasis Rivers, and their tributaries (Figure 1). In the Saint John River, the salt wedge extends upriver to the inflow of Bellisle Bay at approximately river kilometer (RKM) 45. In the Kennebecasis River, brackish water can be detected as far upriver as the confluence with the Hammond River at approximately RKM 30 (Metcalf et al. 1976). The upriver portions of both rivers include dynamic channels, marshlands, and lakes.

Sturgeon aggregation sites in both rivers occur at the boundary of brackish water.

Bottom salinities at these two sites are typically at or below 15 ppt (Trites 2011). At one site, near the Mistake Cove peninsula in the Saint John River, the channel narrows causing relatively high flows with a maximum depth of 12 m in the channel. Along the peninsula, depths range from 1 to 5 m, have fine silt substrate, and abundant macrophytes in summer months. At Perry Point in the Kennebecasis River, the high flows below the confluence with the Hammond River drain into an open fjord habitat, ranging from 2 to 5 m deep, before entering the main stem

Kennebecasis River. The fjord ends at a steep sill where depth increases sharply to 7 m and continues to increase until reaching depths of 30 m and more in the downstream channel.

Fish capture and tagging

We captured juvenile Atlantic sturgeon using 50 m bottom-set gill nets with 6 cm stretch mesh. Soak times ranged from one to two hours and sampling was conducted from May to June in 2016. Fishing effort was distributed throughout the river, however, all fish used in this study were captured at Mistake Cove in the Saint John (SJR) and Perry Point in the Kennebecasis River (KEN). Juvenile sturgeon were transferred directly from the net to an on-board holding tank for transport to shore. All fish were weighed and measured for total length (TL), fork length (FL), and girth. Each fish was tagged with a T-bar anchored floy tag and a passive integrated transponder (PIT) tag (Biomark HPT12) for future identification.

Juvenile Atlantic sturgeon that were less than 100 cm TL and in good condition were selected for acoustic tagging. Fish with regular opercular beats that were able to maintain orientation were determined to be in good condition. Fish were anesthetized with 80 mg/L methane sulfonate (MS-222) buffered 2:1 with sodium bicarbonate (NaHCO_3), in accordance with the Atlantic sturgeon research techniques outlined by NOAA (2010). To reduce recovery time, we used the lowest possible dosage while still observing loss of motor function. Loss of equilibrium typically occurred between 5 and 10 minutes. During the surgical procedure, fish were placed in a v-trough over a freshwater holding tank and intubated with freshwater using a recirculating system. A 3-cm incision was made ventrally between scutes four and five anterior to pelvic fin insertion to the left of the ventral line. Acoustic tags were sanitized using 90% ethanol, wiped clean, and inserted into the body cavity. When the body cavity wall was sufficiently thick, we used a single interrupted suture to secure the tag internally following the

surgical protocol outlined in Crossman et. al. (2013). The surgical procedure typically lasted between three and five minutes. Fish recovered in a freshwater holding tank before being released from shore, just downstream of the capture location. Recovery typically took between 10 and 15 minutes.

We tagged a total of 19 Atlantic sturgeon juveniles in 2016 using Vemco coded acoustic tags (Table 1); 10 and 9 fish were tagged in the Saint John and Kennebecasis Rivers respectively. Fish size ranged from 44 to 83 cm fork length (FL) with the smallest fish receiving the V9 and V9P tags. Tags emitted a signal at a random interval between nominal delay $\pm$ (1/2) nominal delay. Tag weight did not exceed the standard 2% of body weight (mean $\pm$ standard deviation $0.40 \pm 0.11\%$) (Winter 1983).

Data collection and processing

We used an array of seven Vemco VR2TX acoustic receivers to measure fine-scale movement at two aggregation sites in the Saint John and Kennebecasis Rivers (Figure 1). The array was deployed once during summer and fall of 2016 at each site (Table 2). Receivers were attached to anchor lines, secured to moorings, and floated with a buoy approximately 1.5 m above the river bottom. Each VR2TX receiver is equipped with an internal V16 synchronization tag, allowing for the calibration of receiver timing and position calculation during Vemco VPS processing. Receivers were deployed at distances of 600 m or less from neighboring receivers. At Perry Point, the receiver array was approximately 1,000 m long and 400 m wide; at Mistake Cove, the array was approximately 1,200 m long and 500 m wide. A maximum distance of 600 m enabled full coverage of the aggregation area (determined from active tracking) while also allowing for tagged fish to be detected by at least three receivers simultaneously. Vemco calculated fish position using the time differential of signal detection at three or more receivers. Fish position

was calculated to within one meter with an associated horizontal position error (HPE), a radius of error surrounding each position estimate (Smith 2013). Data were then filtered by removing any fish position with an HPE greater than 20. The HPE 20 filter minimized positional error while maximizing the number of detections of roughly equal confidence included in the analysis.

Data analysis

Following VPS processing, calculated positions were assigned to one of three photoperiods: day, night, and crepuscular. Detections occurring from two hours after sunrise to two hours before sunset were categorized as day; those occurring from two hours after sunset to two hours before sunrise were categorized as night; and those occurring during a two-hour window before and after sunrise and sunset were categorized as crepuscular. Straight trajectories through the site, exhibiting no aggregation behavior, were eliminated from the analysis to prevent overestimating space use.

We used R statistical software and the t-LoCoH package to construct convex hulls around point sets that are localized in space and time (Lyons et al. 2013). A convex hull is the smallest possible polygon that can be drawn around a set of nearest neighbors; hulls are sorted and aggregated to construct isopleths that describe space use. Unlike traditional utilization distribution methods, t-LoCoH integrates time into neighbor selection and hull sorting, which allows for temporal partitioning of space use and calculation of movement metrics, such as revisitation rates and duration of stay. T-LoCoH is superior to kernel density estimators in defining boundaries and excluding unused areas from home range estimates, making it well-suited for evaluating collective space use of fish species (Getz et al. 2007; Doherty et al. 2017).

Time is incorporated through a user-defined, scaling parameter, s , which controls the extent to which time should be considered in nearest neighbor selection. Given the focus on sub-

daily patterns of space use, s was selected such that time and space terms were equalized within eight-hour time periods. This means that points separated by more than eight hours in time will not be considered nearest neighbors regardless of proximity in space. To determine the correct s value for each dataset, we followed recommended guidelines and plotted s values that balanced space and time across a range of time periods (Lyons et al. 2013).

The α -method of nearest neighbor selection is preferable when point density is uneven across space, as it is in these aggregation sites. We set α such that 80% of hulls were constructed using a minimum of 18 nearest neighbors localized in space and time. The number of nearest neighbors was determined by following the minimum spurious hole covering rule outlined by Getz and Wilmers (2004). We constructed hulls and isopleths based on point density, eccentricity (directional movement), revisitation, and duration of stay in order to identify pathways and areas of use within sites. Revisitation is calculated from a user-defined parameter, inter-visit gap (IVG), which determines how long a fish must be absent from a hull to be considered a separate visit. Given the high ping rates of these acoustic tags, we set IVG to two hours, which is sufficient time for fish to traverse the site and return to a specific area. Revisitation and duration metrics allow for the characterization of space use within aggregation sites. High revisitation rates are characteristic of regular exploitation of resources while high duration is characteristic of station-holding behavior (Lyons et al. 2013). Eccentricity can be used to identify pathways of directional movement within aggregation sites.

We used non-metric multidimensional scaling (NMDS) to test for differences in spatiotemporal distribution, eccentricity, revisitation, and duration of stay between sites and seasons. Isopleths are constructed from aggregating hulls and estimate space use and movement behaviors across aggregation sites. Isopleth metrics include hull area, hull perimeter, number of

enclosed points, proportion of total points, and hull value last added to the isopleth; these are calculated at 10%, 25%, 50%, 75%, and 95% isopleth levels. The area covered by a 50% isopleth is considered the core area, while the 95% isopleth is considered home range within the site. The data were standardized and fourth-root transformed prior to creating matrices of Euclidean distance. The fourth root transformation was used to control for the disproportionate effect of extreme values on ordinations (Legendre and Legendre 2012). We constructed ordinations from 999 permutations and used Analysis of Similarities (ANOSIM) to test for differences between distance matrices. ANOSIM pairwise comparisons were used to test for differences between sites, seasons, interactions between site and season, as well as photoperiods.

Results

Across summer and fall, 7 of 9 KEN fish used the Perry Point aggregation site and 7 of 10 of SJR fish used the Mistake Cove site (Table 3). There was no movement between aggregation sites, although one KEN fish was observed in the vicinity of the Mistake Cove site for a short period of time (< 10 minutes). In both sites, three fish were consistently located at the site in both summer and fall. The number of tagged fish located at an aggregation site did not exceed 6 at any point. All SJR fish were detected in the SJR array; however, three fish made clear, straight trajectories through the site, exhibiting no aggregation behavior, and were eliminated from analysis to avoid overestimating space use.

There was a shift in core area and overall point density between summer and fall in Mistake Cove (Figure 2). Summer core area was tightly distributed along the northwestern shore of the Mistake Cove peninsula with relatively few paths across the channel. The fall core area lies along the opposite, southeastern shore with increased cross-channel paths. The 10-75% isopleths are contracted as compared to summer and the 95% isopleth has expanded to include

242 some use of channel and summer core areas. Core area decreased by more than 50% from
243 summer to fall while the number of points enclosed increased, indicating more concentrated
244 space use (Table 4).

245 Both core area location and space use shifted between summer and fall in Mistake Cove.
246 The summer core area of Mistake Cove is characterized by high revisitation rates and low to
247 moderate duration of stay while upper isopleth areas are characterized by low to moderate
248 revisitation and low duration of stay (Figure 3). The fall core area is characterized by moderate
249 revisitation and moderate duration within the contracted core area; the 75% and 95% isopleths
250 show low revisitation and low duration of stay, with the exception of one small, off-channel area
251 showing very high duration of stay. An NMDS ordination of site and season shows some overlap
252 in Mistake Cove summer and fall density isopleth metrics (Figure 4). Pairwise comparisons show
253 significant differences between summer and fall density isopleths (ANOSIM $R = 0.1340$, $p =$
254 0.03) and revisitation rates (ANOSIM $R = 0.1305$, $p = 0.02$); however, duration of stay was not
255 significantly different between seasons (ANOSIM $R = 0.0198$, $p = 0.24$). Fall space use is
256 heavily skewed by high residency of a single fish. Eliminating this fish from the dataset yielded a
257 similar pattern. The high density 10% isopleth remained adjacent to the southeastern shore but
258 core areas were larger and isopleth distribution was more disperse, likely due to the relatively
259 low number of points from the remaining three fish.

260 There was no clear shift in space use in Perry Point between summer and fall. The 50%
261 and 95% isopleths were contracted in summer compared to fall but core areas remained close to
262 the aggregation site center (Figure 5). Core area increased by over 50% from summer to fall
263 while the number of enclosed points decreased, indicating more dispersed space use in fall.

Space use shifted in Perry Point between summer and fall. The summer 10% isopleth is characterized by moderate revisitation and high duration of stay, surrounded by the 50% isopleth, which is characterized by high revisitation and low to moderate duration of stay (Figure 6). Surrounding isopleths have moderate revisitation and low duration of stay. The fall core area is characterized by high revisitation and low duration of stay surrounded by upper isopleths showing moderate revisitation and low duration. There are two areas within the 75% and 95% isopleths that show very low revisitation and the highest duration of stay. The NMDS ordination shows Perry Point summer and fall hull metrics to be well separated. There were significant differences between seasons in density isopleths (ANOSIM $R = 0.2151$, $p = 0.008$), revisitation rates (ANOSIM $R = 0.1667$, $p = 0.01$), and duration of stay (ANOSIM $R = 0.1421$, $p = 0.024$).

Space use was similar between Mistake Cove and Perry Point in summer but diverged in fall. Pairwise comparisons of summer hull metrics between sites yielded no significant results; however, comparisons of fall hull metrics revealed significant differences in density isopleths (ANOSIM $R = 0.4021$, $p = 0.001$), revisitation rates (ANOSIM $R = 0.2378$, $p = 0.004$), and duration of stay (ANOSIM $R = 0.2979$, $p = 0.002$).

Eccentricity, or directional movement, in Mistake Cove is largely restricted to shoreline areas and parallel to flow, with few hulls crossing the channel. Directionality within Perry Point is both parallel and perpendicular to flow, with hulls more evenly distributed across the site (Figure 7). Sites did not differ between seasons; however, sites were significantly different from each other in both summer (ANOSIM $R = 0.1060$, $p = 0.031$) and fall (ANOSIM $R = 0.1454$, $p = 0.008$).

Calculated positions and point densities appeared to be evenly distributed across day, night, and crepuscular periods (Figure 2; Figure 3). NMDS ordinations of both photoperiod and

photoperiod by season showed nearly complete overlap and analysis of similarities yielded no significant results (Table 5).

Discussion

Juvenile Atlantic sturgeon aggregation behavior and space use vary between sites and seasons. Aggregation sites were predominantly characterized by two types of space use: high density areas where juveniles stayed for long periods and 2) low density areas that were revisited frequently and juveniles remained for very short periods. This high revisitation, short duration pattern may be indicative of searching and foraging behavior. This suggests juveniles may be aggregating in small, high density areas adjacent to foraging grounds. It is possible that resource distribution is a driver of fine-scale space use and could explain the cross-channel shift of core area in Mistake Cove between summer and fall.

Aggregation behavior of juvenile and adult Atlantic sturgeon is well-documented at coarse scales (Moser and Ross 1995; Hatin et al. 2007; Fernandes et al. 2010) but there has been no investigation of distribution and space use at fine-scales (< 1 km) to this point. Previous investigations of juvenile and adult Atlantic sturgeon have found that coarse-scale distribution corresponds to that of high density prey (Fox et al. 2002; Stein et al. 2004; Hatin et al. 2007; Novak et al. 2017) and juveniles typically aggregate near the freshwater-saltwater interface (Lazzari et al. 1986; Moser and Ross 1995; Hatin et al. 2007). This is consistent with the aggregation sites identified in SJR and KEN, as both sites are located near the saltwater-freshwater interface with bottom salinity typically at or below 15 ppt (Trites 2011).

Seasonal space use

Seasonal use of aggregation sites has been documented for Atlantic sturgeon adults and subadults (Fernandes et al. 2010; Taylor et al. 2016). Differences between summer and fall distribution and

aggregation behavior at both sites suggests juveniles may shift aggregation sites seasonally as well. The larger home range, higher revisitation, and lower duration of stay in Perry Point during fall could be indicative of a shifting of core area outside of receiver range but continued use of the site as foraging grounds. It is possible that juveniles aggregate in entirely different locations during winter months. High densities of juveniles from both rivers have been observed in lower reaches of the Saint John estuary (Bell 2011) and coarse-scale movement data indicates residence at both aggregation sites decreases substantially in the winter and early spring (Whitmore, unpublished data). Fall may therefore represent a transitional period, when juveniles are more active and moving to more suitable winter habitat.

Seasonal aggregations are relatively common in marine and estuarine species. Sex-specific feeding and social aggregations have been documented for catsharks (*Scyliorhinus canicular*) (Jacoby et al. 2010) and white sharks (*Carcharodon carcharias*) (Bruce and Bradford 2015). Aggregations of Atlantic cod (*Gadus morhua*) and American plaice (*Hippoglossoides platessoides*) shift seasonally with food resources and water temperature (Swain et al. 1998). It is possible that juvenile Atlantic sturgeon move to deeper, relatively warmer aggregation areas in the lower river during cold months. Future research should focus on investigating sturgeon social structure, identifying winter and spring aggregation sites, and association with habitat characteristics.

Directional movement

Directional movement, or eccentricity, was consistent between seasons but different between aggregation sites, suggesting flow is an important driver of space use at fine scales but not necessarily of site selection at coarse scales. The Mistake Cove site is within a comparatively narrow stretch of river where flows would be expected to increase. Directional movement

appears to be predominantly along the shoreline and parallel to flow with very little cross-channel movement. The Perry Point site is downstream from the confluence of the Kennebecasis and Hammond Rivers where the channel widens into an extensive, shallow fjord with relatively low flows. Directional movement within Perry Point is much more evenly distributed across the site and directionality is inconsistent. Flow is generally thought to be an important driver of habitat selection by sturgeon species. Previous work found high densities of juvenile Atlantic sturgeon in a similar depth range, in areas of low bottom flow near channel habitat, and distant from shoreline (Hatin et al. 2007). Studies of habitat selection by adult and subadult Atlantic sturgeon typically find fish associated with areas of low flow and fine sediment (USACE 1989; Savoy and Pacileo 2003). Juvenile Atlantic sturgeon habitat selection may be driven by substrate and salinity at coarse-scales while current velocity and resource distribution drive distribution at fine scales.

Diel activity patterns

Distribution and behavior were consistent across photoperiods. Calculated positions and hull densities were similar across day, night, and crepuscular periods and did not support our hypothesis. Adult Atlantic sturgeon have been shown to exhibit higher crepuscular activity during intertidal foraging (McLean et al. 2014). McLean et al. 2014 suggested higher activity levels during dawn and dusk are driven by prey abundance and distribution in the intertidal zone. Although there has been very little investigation into juvenile sturgeon activity levels overall, Jordan et al. (2006) found juvenile pallid sturgeon activity levels to be consistent across photoperiods. Juvenile and adult sturgeon may exhibit differential patterns of diel activity, possibly related to diet and foraging opportunities. It is also possible that individual activity levels and rates of movement differ between periods but collective distribution and aggregation

behavior does not. Ontogenetic shifts in diel activity patterns are common across species, typically driven by feeding ecology or predator avoidance (Helfman 1986). Future research will focus on individual trajectories and seek to identify differences in individual activity levels across photoperiods.

Atlantic sturgeon migration behavior can exhibit a pattern of long-distance movement followed by localized movement within high-residency areas (Fox et al. 2002; Hatin et al. 2002). We focused on movement and distribution within newly identified aggregation sites to explore fine-scale space use in greater detail. This is one of few studies investigating the juvenile life stage of Atlantic sturgeon and the first to examine space use in aggregation sites. Our results reveal a diversity of space use at fine scales and can help frame questions regarding social structure, feeding ecology, bioenergetics, and habitat preference of sturgeon species. Future work should employ longer duration receiver deployments across seasons and habitat surveys to determine long-term patterns and habitat associations.

Understanding aggregation behavior and space use can aid sustainable management of the species throughout its range. Elasticity analysis of Atlantic sturgeon has revealed juvenile survival makes the greatest contribution to population growth (Gross et al. 2002). Conservation efforts focusing on protection of juvenile aggregation areas could therefore lead to substantial population gains. Management recommendations based on coarse-scale distributions suggest area closures on the scale of river reach (Collins et al. 2000; Dunton et al. 2015). These results suggest management actions could be effective at much finer spatiotemporal scales, potentially making management and enforcement more feasible.

Acknowledgements

378 This research was made possible by funding from Ocean Tracking Network, New Brunswick
379 Wildlife Trust Fund, New Brunswick Innovation Fund, Canadian Foundation for Innovation, and
380 National Science and Engineering Research Council of Canada Discovery and Research, Tools
381 and Instruments grants to MKL. Clay Steell, Christine Gilroy, Matthew Brown, and Andrew
382 Taylor assisted with field work.

Draft

References

- Bell, J.W. 2011. Acoustic telemetry and stable isotope analysis of Atlantic sturgeon juveniles, *Acipenser oxyrinchus*, in the Saint John River, New Brunswick, Canada. Honors Thesis, Department of Biology, Mount Allison University, Sackville, NB.
- Bruce, B., and Bradford, R. 2015. Segregation or aggregation? Sex-specific patterns in the seasonal occurrence of white sharks *Carcharodon carcharias* at the Neptune Islands, South Australia. *J. Fish Biol.* 87: 1355-1370.
- Collins, M.R., Rodgers, S.G., Smith, T.I.J., and Moser, M.L. 2000. Primary factors affecting sturgeon populations in the southeastern United States: fishing mortality and degradation of essential habitats. *Bull. Mar. Sci.* 66:917-928.
- Crossman, J.A., Hammell, L.K., and Litvak, M.K. 2013. Experimental examination of surgical procedures for implanting sonic transmitters in juvenile shortnose sturgeon and Atlantic sturgeon. *North American Journal of Fisheries Management* 33:549-556.
- Dadswell, M.J. 2006. A review of the status of Atlantic sturgeon in Canada, with comparisons to populations in the United States and Europe. *Fisheries* 31:218-229.
- Department of Fisheries and Oceans (DFO). 2013. Recovery potential assessment for Atlantic sturgeon (Maritimes Designatable Unit). DFO Canadian Scientific Advisory Report 2013/022.
- Doherty, P.D., Baxter, J.M., Godley, B.J., Graham, R.T., Hall, G., Hall, J., Hawkes, L.A., Henderson, S.M., Johnson, L., Speedie, C., Witt, M.J. 2017 Testing the boundaries: Seasonal residency and inter-annual site fidelity of basking sharks in a proposed Marine Protected Area. *Biological Conservation* 209: 68-75.

- Dunton, K.J., Jordaan, A., Mckown, K., Conover, D.O., and Frisk, M. 2010. Abundance and distribution of Atlantic sturgeon (*Acipenser oxyrinchus*) within the Northwest Atlantic Ocean, determined from five fishery-independent surveys. *Fish. Bull.* 108:450-465.
- Dunton, K.J., Jordaan, A., Conover, D.O., McKown, K.A., Bonacci, L.A., and Frisk, M.G. 2015. Marine distribution and habitat use of Atlantic sturgeon in New York lead to fisheries interactions and bycatch. *Marine and Coastal Fisheries: Dynamics, Management, and Ecosystem Science* 7:18–32
- Erickson, D., Kahnle, A., Millard, M.J., Mora, E.A., Bryja, M., Higgs, A., Mohler, J., DuFour, M., Kenney, G., Sweka, J., and Pikitch, E.K. 2011. Use of pop-up satellite archival tags to identify oceanic-migratory patterns for adult Atlantic sturgeon, *Acipenser oxyrinchus oxyrinchus* Mitchell, 1815. *J. Appl. Ichthyol.* 27:356–365.
- Fernandes, S.J., Zydlewski, G.B., Zydlewski, J.D., Wippelhauser, G.S., and Kinnison, M.T. 2010. Seasonal distribution and movements of shortnose sturgeon and Atlantic sturgeon in the Penobscot River estuary, Maine. *Trans. Am. Fish. Soc.* 5:1436-1449.
- Fox, D.A., Hightower, J.E., and Parauka, F.M. 2002. Estuarine and nearshore marine habitat use by gulf sturgeon from the Choctawhatchee River system, Florida. *Proceedings of the American Fisheries Society Symposium.* 28:111–126.
- Getz, W.M. and Wilmers, C.C. 2004. A local nearest-neighbor convex-hull construction of home ranges and utilization distributions. *Ecography* 27: 489-505.
- Getz, W.M., Fortmann-Roe, S., Cross, P.C., Lyons, A.J., Ryan, S.J., and Wilmers, C.C. 2007. LoCoH: nonparametric kernel methods for constructing home ranges and utilization distributions. *PLoS One* 2:e207.

- Jordan, G.R., Klumb, R.A., Wanner, G.A., and Stancill, W.J. 2006. Poststocking movements and habitat use of hatchery-reared juvenile pallid sturgeon in the Missouri River below Fort Randall Dam, South Dakota and Nebraska. *Trans. Am. Fish. Soc.* 135: 1499-1511.
- Gross, M.R., Repka, J., Robertson, C.T., Secor, D.H., and Van Winkle, W. 2002. Sturgeon conservation: insights from elasticity analysis. In: Van Winkle, W., Anders, P.J., Secor, D.H., and Dixon, D.A. (eds) *Biology, management, and protection of North American sturgeon*. American Fisheries Society, Symposium 28, Bethesda, MD 13-30.
- Hale, E.A., Park, I.A., Fisher, M.T., Wong, R.A., Strangl, M.J., and Clark, J.H. 2016. Abundance estimate for and habitat use by early juvenile Atlantic sturgeon within the Delaware River estuary. *Trans. Am. Fish. Soc.* 145:1193-1201.
- Hatin, D., Fortin, R., and Caron, F. 2002. Movements and aggregation areas of adult Atlantic sturgeon (*Acipenser oxyrinchus*) in the St. Lawrence River estuary, Quebec, Canada. *J. Appl. Ichthyol.* 18:586-594.
- Hatin, D., Munro, J., Caron, F., and Simons, R.D. 2007. Movements, home range size, and habitat use and selection of early juvenile Atlantic sturgeon in the St. Lawrence estuarine transition zone. In: Munro, J., Hatin, D., Hightower, J.E., McKown, K., Sulak, K.J., Kahnle, A.W., Caron, F. (eds) *Anadromous sturgeons: habitats, threats, and management*. American Fisheries Society, Symposium 56, Bethesda, Maryland 129-155.
- Helfman, G.S. 1986. Fish behavior by day, night, and twilight. In: Pitcher, T.J. (ed) *The behavior of teleost fishes*. Springer, United States 366-387.
- International Union for the Conservation of Nature (IUCN). 2006. IUCN Red List of threatened species. Available from <http://www.iucnredlist.org> [Accessed 8 July 2017]

- Jacoby, D.M.P., Busawon, D.S., and Sims, D.W. 2010. Sex and social networking: the influence of male presence on social structure of female shark groups. *Behavioral Ecology* 21: 808-818.
- Kynard, B., and Horgan, M. 2002. Ontogenetic behavior and migration of Atlantic sturgeon, *Acipenser oxyrinchus oxyrinchus*, and shortnose sturgeon, *A. brevirostrum*, with notes on social behavior. *Environ. Biol. Fishes* 63:137-150.
- Laney, R.W., Hightower, J.E., Versak, B.R., Mangold, M.F., Cole, W., and Winslow, S.E. 2007. Distribution, habitat use, and size of Atlantic sturgeon captured during cooperative winter tagging cruises, 1988-2006. In: Munro, J. (ed) *Anadromous sturgeons: habitats, threats, and management*. American Fisheries Society, Symposium 56, Bethesda, Maryland 167-182.
- Lazzari, M.A., O'Herron, J.C., and Hastings, R.W. 1986. Occurrence of juvenile Atlantic sturgeon, *Acipenser oxyrinchus*, in the upper tidal Delaware River. *Estuaries* 9:356-361.
- Legendre, P., and Legendre, L. 2012. *Numerical Ecology*, 3rd Edition. Elsevier, United Kingdom.
- Lyons, A., Turner, W.C., and Getz, W.M. 2013. Home range plus: a space-time characterization of movement over real landscapes. *Movement Ecology* [online serial] 1:2-14. DOI: 10.1186/2051-3933-1-2.
- McLean, M.F., Dadswell, M.J., and Stokesbury, M.J.W. 2013. Feeding ecology of Atlantic sturgeon, *Acipenser oxyrinchus oxyrinchus* Mitchill, 1815 on the infauna of intertidal mudflats of Minas Basin, Bay of Fundy. *J. Appl. Ichthyol.* 29:503–509.
- McLean, M.F., Simpfendorfer, C.A., Heupel, M.R., Dadswell, M.J., and Stokesbury, M.J.W. 2014. Diversity of behavioural patterns displayed by a summer feeding aggregation of

- Atlantic sturgeon in the intertidal region of Minas Basin, Bay of Fundy, Canada. *J. Appl. Ichthyol.* 496:59-69.
- Moser, M.L., and Ross, S.W. 1995. Habitat use and movements of shortnose and Atlantic sturgeons in the Lower Cape Fear River, North Carolina. *Trans. Am. Fish. Soc.* 124:225-234.
- Metcalfe, C.D., Dadswell, M.J., Gillis, G.F., and Thomas, M.L. 1976. Physical, chemical, and biological parameters of the Saint John River estuary, New Brunswick, Canada. Fisheries and Marine Service Technical Report 686.
- National Oceanic and Atmospheric Administration (NOAA). 2010. Atlantic sturgeon research techniques. NOAA Technical Memorandum NMFS-NE-215.
- National Oceanic and Atmospheric Administration (NOAA). 2012a. Endangered and threatened wildlife and plants; threatened and endangered status for distinct population segments of Atlantic sturgeon in the northeast region. *Federal Register* 77:5880–5912.
- National Oceanic and Atmospheric Administration (NOAA). 2012b. Endangered and threatened wildlife and plants; final listing for two distinct population segments of Atlantic sturgeon (*Acipenser oxyrinchus oxyrinchus*) in the southeast. *Federal Register* 77:5914–5982.
- Novak, A.J., Carlson, A.E., Wheeler, C.R., Wippelhauser, G.S., and Sulikowski, J.A. 2017. Critical foraging habitat of Atlantic sturgeon based on feeding habits, prey distribution, and movement patterns in the Saco River estuary, Maine. *Trans. Am. Fish. Soc.* 146:308-317.

- Patrick, W.S., and Damon-Randall, K. 2008. Using a five-factored structured decision analysis to evaluate the extinction risk of Atlantic sturgeon (*Acipenser oxyrinchus oxyrinchus*). *Biological Conservation* 141:2906-2911.
- Savoy, T., and Pacileo, D. 2003. Movements and important habitats of subadult Atlantic sturgeon in Connecticut waters. *Trans. Am. Fish. Soc.* 132: 1-8.
- Smith, T.I. 1985. The fishery, biology, and management of Atlantic sturgeon, *Acipenser oxyrinchus*, in North America. *Environ. Biol. Fishes* 14:61-72.
- Smith, F. 2013. Understanding HPE in the Vemco Positioning System (VPS). (ed. Vemco) Bedford, NS, Canada.
- Stein, A.B., Friedland, K.D., and Sutherland, M. 2004. Atlantic sturgeon marine distribution and habitat use along the northeastern coast of the United States. *Trans. Am. Fish. Soc.* 133:527-537.
- Swain, D.P., Chouinard, G.A., Morin, R., and Drinkwater, K.F. 1998. Seasonal variation in the habitat associations of Atlantic cod (*Gadus morhua*) and American plaice (*Hippoglossoides platessoides*) from the southern Gulf of St. Lawrence. *Can. J. Fish. Aquat. Sci.* 55: 2548-2561.
- Taylor, A.D., and Litvak, M.K. 2017. Timing and location of spawning based on larval capture and acoustic telemetry of Atlantic sturgeon in the Saint John River, New Brunswick. *Trans. Am. Fish. Soc.* 146: 283-290.
- Taylor, A.D., Ohashi, K., Sheng, J., Litvak, M.K. 2016. Oceanic distribution, behavior, and a winter aggregation area of adult Atlantic sturgeon, *Acipenser oxyrinchus oxyrinchus*, in the Bay of Fundy, Canada. *Plos One* [online serial] DOI: 10.1371/journal.pone.0152470.

Trites, R.W. 1960. An oceanographical and biological reconnaissance of Kennebecasis Bay and the Saint John River estuary. *Journal of the Fisheries and Wildlife Board of Canada* 17:377-408.

The Committee on the Status of Endangered Wildlife in Canada (COSEWIC). 2015. Atlantic sturgeon: consultations on listing under the Species at Risk Act. Fisheries and Oceans Canada. Available from www.sararegistry.gc.ca [Accessed 8 July 2017].

US Army Corps of Engineers (USACE). 1989. Species Profiles: Life Histories and environmental requirements of coastal fishes and invertebrates (Mid-Atlantic Bight), Atlantic and shortnose sturgeon. Biological Report 82, TR EL-82-4.

Waldman, J.R., Hart, J.T., and Wirgin, I.I. 1996. Stock composition of the New York Bight Atlantic sturgeon fishery based on analysis of Mitochondrial DNA. *Trans. Am. Fish. Soc.* 125:364-371.

Winter, J.D. 1983. Underwater biotelemetry. In: Nielson, L.A., and Johnson, D.L. (eds). *Fisheries techniques*. American Fisheries Society, Bethesda, Maryland 371-395.

Wippelhauser, G.S., Sulikowski, J., Zydlewski, J.B., Altenritter, M.A., Kieffer, M., and Kinnison, M.T. 2017. Movements of Atlantic sturgeon of the Gulf of Maine inside and outside of the geographically defined distinct population segment. *Marine and Coastal Fisheries* 9:93-107.

Wirgin, I., Maceda, L., Waldman, J.R., Wehrell, S., Dadswell, M.J., and King, T. 2012. Stock origin of migratory Atlantic sturgeon in Minas Basin, inner Bay of Fundy, Canada, determined by microsatellite and mitochondrial DNA analyses. *Trans. Am. Fish. Soc.* 141:1389-1398.

Table 1. Summary of tag settings. Pressure tags used to measure fish depth are designated with a P; tag power is either high (H) or low (L). Tag settings were configured such that the nominal delay did not exceed 120 seconds and tag life was maximized.

Tag Type	Length (mm)	Weight in Water (g)	Nominal Delay (seconds)	Tag life (days)	Number of fish tagged
V9-2H	29	2.9	90	365	4
V9P-2H	44	3.5	120	252	4
V13-1H	36	6	60	362	7
V13P-1H	48	6.5	90	365	3
V16P-4H	71	11.7	60	1210	1

Table 2. Summary of receiver deployments in each site and season and number of fish using site.					
River	Site	Season	Deployment period	Days deployed	Fish present
SJR	Mistake Cove	Summer	30 Jun – 7 Jul	8	6
	Mistake Cove	Fall	3 Oct – 5 Nov	34	4
KEN	Perry Point	Summer	22 Jul – 2 Aug	12	4
	Perry Point	Fall	14 Sep – 1 Oct	18	6

Draft

Table 3. Individual fish presence, fish size, detection days, number of detections, cumulative time spent within the site, and number of times fish exited and re-entered by site and season. Fish identification numbers in bold were present at a site in both summer and fall.

Site	Fish ID	Fork length (cm)	Days detected	Number detections	Cumulative time detected (hours)	Exits and re-entries (#)	Total detection (days) #
Mistake Cove (summer)	41711	44	7	1943	140.1	1	
	41712	55	2	78	9.2	0	
	43521	59	8	4245	145.7	2	
	1935	72	8	1998	119.0	6	
	1936	63	2	149	17.0	1	
	2064	56	2	83	12.8	1	(29) 8496
Mistake Cove (fall)	43516	58	26	9789	412.7	13	
	1935	72	2	177	10.1	1	
	1936	63	1	236	9.8	0	
	2064	56	6	307	34.1	6	(35) 10509
Perry Point (summer)	43515	71	12	2918	173.7	12	

	43517	63	12	3097	212.8	8	
	43519	61	4	32	1.8	0	
	2062	66	12	718	139.7	14	(40) 6765
Perry Point (fall)	43515	71	3	354	23.9	2	
	43518	68	2	127	9.0	4	
	43519	61	10	708	59.9	12	
	12762		11	2164	93.0	13	
	1937		4	176	17.3	3	
	2062		18	749	167.3	18	(48) 4278

Table 4. Areas and number of enclosed points of home range (95%) and core areas (50%) across aggregation sites					
Site	Season	Density isopleth area (m ²)		Number of enclosed points	
		50%	95%	50%	95%
Mistake Cove (SJR)	Summer	211	462	4486	8107
Mistake Cove (SJR)	Fall	102	605	5562	9984
Perry Point (KEN)	Summer	201	511	3389	6454
Perry Point (KEN)	Fall	415	689	2152	4112

Table 5. NMDS and ANOSIM R for isopleth metrics by site, season, and photoperiod. Site-season values are tests of the interaction between aggregation site and season. Starred p-values are significant

Test	Hull Type	ANOSIM R	p-value
Site	Density	0.1023	0.006 *
	Eccentricity	0.1257	0.003 *
	Revisitation	0.0707	0.022 *
	Duration	0.1222	0.007 *
Season	Density	0.0394	0.082
	Eccentricity	0.0095	0.246
	Revisitation	0.0666	0.029 *
	Duration	0.0123	0.223
Photoperiod	Density	-0.0320	0.951
	Eccentricity	-0.0336	0.989
	Revisitation	-0.0202	0.801
	Duration	-0.0315	0.962
Site - Season	Density	0.1808	0.001 *
	Eccentricity	0.0927	0.004 *
	Revisitation	0.1459	0.002 *
	Duration	0.1284	0.004 *

Figure Captions

Figure 1. Map of the lower Saint John River Basin with receiver locations at two aggregation sites, Mistake Cove (blue) and Perry Point (green). Map data: Google, DigitalGlobe.

Figure 2. Calculated positions (left) and density isopleths (right) in the Mistake Cove aggregation site in the Saint John River in summer (top) and fall (bottom). The scaling parameter (s) balances space and time in point selection during hull construction. The time-scaled distance metric (a) is a non-physical distance between parent points and nearest neighbors and is constrained so that each hull has a minimum of 18 nearest neighbors. Map data: Google, DigitalGlobe.

Figure 3. Visitation rate (left) and duration of visit (right) in the Saint John River aggregation site at Mistake Cove in summer (top) and fall (bottom). Visitation rate is defined by an inter-visit gap (IVG) of 7200 seconds (2 hours). Map data: Google, DigitalGlobe.

*Fall visitation rate was plotted using IVG = 5 hours due to high revisitation in core areas

Figure 4. NMDS ordination of point density isopleth metrics by site and season.

Figure 5. Calculated positions (left) and density isopleths (right) in the Perry Point aggregation site in the Kennebecasis River in summer (top) and fall (bottom). The scaling parameter (s) balances space and time in point selection during hull construction. The time-scaled distance metric (a) is a non-physical distance between parent points and nearest neighbors and is constrained so that each hull has a minimum of 18 nearest neighbors.

Figure 6. Visitation rate (left) and duration of visit (right) in the Kennebecasis River aggregation site at Perry Point in summer (top) and fall (bottom). Visitation rate is defined by an inter-visit gap (IVG) of 7200 seconds (2 hours).

*Summer and fall visitation rate had to be plotted using IVG = 5 hours and IVG = 6 hours, respectively, due to high revisitation in core areas.

Figure 7. Eccentricity isopleths of Mistake Cove (top) and Perry Point (bottom) aggregation sites in summer (left) and fall (right). Eccentricity represents directionality of fish movement within each aggregation site.

Draft