RESEARCH

Use of social network analysis to examine preferential co-occurrences in Atlantic Sturgeon *Acipenser oxyrinchus oxyrinchus* Mitchill, 1815

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Abstract

Background: Application of Social Network Analysis (SNA) to acoustic telemetry is a useful approach to examine social behavior in fish. Atlantic Sturgeon (*Acipenser oxyrinchus oxyrinchus*) are ancient, long-lived anadromous finfish. Although Atlantic Sturgeon have been the subject of numerous telemetry studies, none have used SNA to analyze their co-occurrence behavior. During 2010–2014 Atlantic Sturgeon ($n = 103$) that were later genetically identified as being from the Saint John River, Canada and the Kennebec River, US were captured by otter trawl and brush weir in Minas Basin, Bay of Fundy, Canada, and acoustically tagged. Using data from moored acoustic receivers within foraging habitat in Minas Basin, we tested if Atlantic Sturgeon formed social associations that were random or structured during 2012 to 2014; and whether these co-occurrences consisted of individuals from the same river of origin or capture date.

Results: Irrespective of genetic origin and initial capture date, Atlantic Sturgeon formed co-occurrences in Minas Basin that were significantly different than would be observed by chance during 2012 and very close to significant during 2013. Analysis demonstrated that some Atlantic Sturgeon preferentially co-occur within their primary feeding habitat.

Conclusions: The current threats to Atlantic Sturgeon aggregations within the Bay of Fundy, Nova Scotia, include bycatch in fisheries throughout their coastal migration routes and more recently the development of tidal turbines along their migratory corridor to their summer aggregation site. It is important to determine if Atlantic Sturgeon form aggregations with conspecifics from the same population to inform management decisions regarding threats to groups of individuals. This study indicated that Atlantic Sturgeon may form preferential co-occurrences within their feeding aggregation and co-occurrences that were identified were not dependent upon population of origin or initial capture date.

Keywords: *Acipenser oxyrinchus oxyrinchus*, Social network analysis, Minas Basin, Migration, Acoustic telemetry

Background

Forming aggregations or groups with members of the same species is common within the animal kingdom [1]. Aggregations form when individuals from the same species utilize critical habitat including feeding, spawning and overwintering sites [2, 3]. Co-occurrence behavior is highly dependent on the niche utilized by a species, and individual behavioral preferences [4]. Within

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aggregations individuals can display preferential co-occurrences with specific individuals [5]. Preferential co-occurrences describe two individuals associating in a group more often than would be observed by chance [6]; these are categorized as representing social groups [5]. When individuals are passively sharing time and space and do not display a preference for whom they associate with then this is referred to as an aggregation [5].

Prior to the last decade, research concerning the formation of complex social groups has been limited to studies on terrestrial and marine mammals [7–9]. Excluding studies on collective behavior and schooling, fishes' ability for complex social behavior has received little attention [10]. Most studies have been conducted with shoaling species in a controlled laboratory or field setting [11–14], where the researcher can actively observe intraspecific interactions leading to a need to better understand associative behavior in large free-ranging fishes [15].

Social Network Analysis (SNA) is a primary method used to analyze the temporal and spatial patterns within animal populations [16]. SNA theory assumes that two individuals co-occur if they are within close enough temporal and spatial proximity to interact or associate [17]. SNA requires the time-stamped observations of interactions between individuals, and thus has traditionally been applied in observational studies [17–20]. Although interactions are difficult to define, the development of acoustic telemetry has enabled researchers to utilize SNA to estimate the strength and characteristics of interindividual co-occurrence between fishes [21, 22]. Acoustic telemetry involves the use of individuals that are equipped with uniquely coded acoustic transmitters coupled with acoustic receiving devices that are strategically placed enabling researchers to follow organisms across space and time [23, 24]. Co-occurrence strength can be determined based upon the frequency of co-occurrences at acoustic receivers [10]. For species that utilize small home ranges in regions that are densely populated with receivers, researchers can more accurately define social groups [6]. However, for large free-ranging fishes that occupy a diverse range of habitats with varying receiver coverage it is difficult to determine the degree of sociality expressed between organisms [15]. In free-ranging species SNA can be used to identify trends in aggregation behavior based on spatio-temporal co-occurrences between individuals [6, 10, 25].

In this study SNA was used to identify patterns in co-occurrences in a large free-ranging chondrostean, the Atlantic Sturgeon (*Acipenser oxyrinchus oxyrinchus* Mitchill, 1815). Atlantic Sturgeon are an ancient, long-lived (+60 years) anadromous species with a spawning range extending from the Gulf of St. Lawrence, Quebec,

Canada, to the St. John River, Florida, US [26]. In Canada, management recognizes two Designatable Units (DU) of Atlantic Sturgeon. One DU originates from the Saint John River (SJR), New Brunswick, and the other from the Saint Lawrence River, Quebec. In the US, five Distinct Population Segments (DPS) were listed under the Endangered Species Act (ESA) in 2012. These include the Carolina, Chesapeake, New York Bight, and South Atlantic DPS which are listed as endangered and the Gulf of Maine DPS which is listed as threatened [27, 28].

Fisheries' closures and habitat restoration have led to encouraging results including slight increases in the abundance of some populations [29]. Recovery of sturgeon is slow, however, primarily due to life-history traits like late age of maturity that results in delayed recruitment to the population [29]. Age of maturity and timing of spawning for Atlantic Sturgeon are dependent on latitude with northern populations reaching sexual maturity between 20 and 25 years of age [29]. Between spawning, which occurs every 1–4 years, adult Atlantic Sturgeon migrate along the Atlantic coast to feed in non-natal estuaries and tidal embayments in the spring and summer and south during the fall and winter [30]. Starting in May each year approximately 10,000 Atlantic Sturgeon migrate through Minas Passage (MP) into Minas Basin (MB; [31]), Nova Scotia, to feed on abundant benthic invertebrates in the tidal flats [32]. Genetic analyses indicate that the summer feeding aggregation of Atlantic sturgeon in MB is composed of sturgeon from several populations. Sixty-one percent of Atlantic Sturgeon collected with trawls and weirs in MB originated from the SJR, 34% from the Kennebec River (KR), 2% from the Hudson River, New York, and 1% from the James River, Virginia [33].

The KR population of Atlantic Sturgeon has been reported to enter MB earlier in June than the SJR population, and both populations depart during September [34]. Atlantic Sturgeon spend most of their time in the Southern Bight of MB and individuals have been captured together during consecutive sampling years [34]. It is unknown whether the Atlantic Sturgeon captured together were from the same population, and whether they remained together outside of MB [34].

Atlantic Sturgeon from the same population are subject to many stressors throughout their migratory range, including mortality due to bycatch in trawl and gill net fisheries throughout the mid-Atlantic Bight, US [35] and the potential future installation of in-stream tidal power in important migratory corridors. Understanding the co-occurrence patterns of Atlantic Sturgeon is important to help determine if one population or cohort could be disproportionately affected by anthropogenic stressors, such as fisheries' by-catch [36], or interaction with coastal

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engineering projects such as tidal turbines [37], and will hopefully lead to important management discussions about the protection of transboundary species. For larger free-ranging fishes, forming social groups has been predicted to assist in the guided learning of essential habitats [38]. In this study, we sought to (1) describe patterns in co-occurrences between Atlantic Sturgeon aggregating within MB, and assess whether Atlantic Sturgeon form social groups, and (2) to determine if aggregations were more likely to form between individuals from the population or with the same initial capture date.

Results

Atlantic Sturgeon attributes Minas Passage/Minas Basin

During 2010 to 2014, 103 Atlantic Sturgeon were captured via research directed otter trawl ($n = 78$) and brush weir ($n = 25$). Sturgeon had an average ($\pm$ SD) L_F of 134.49 ± 2.03 cm. Atlantic Sturgeon were detected within MB from May to October but detections peaked during May and July (Fig. 1). The mean ($\pm$ SD) number of days that Atlantic Sturgeon were detected within MB during 2012–2014 ranged between 5.9 ± 5.8 (2014) and 14.6 ± 10.8 (2012; Table 1). Most detected Atlantic Sturgeon within MB were genetically assigned to the SJR and classified as sub-adults (< 150 cm L_F; Table 1). During 2014, tags implanted in sturgeon between 2010 and 2013 were still active.

Social network analysis

Atlantic Sturgeon appeared to experience considerable spatial overlap in the time they spent within MB, suggesting that there were enough data to test whether Atlantic Sturgeon preferentially co-occur (Fig. 2). The number of Atlantic Sturgeon dyads detected within MB peaked at 339 in 2012. Most Atlantic Sturgeon detected within MB co-occurred with another specimen but exhibited a low degree of co-occurrence (Table 2; Fig. 3).

Table 1 Characteristics of Atlantic Sturgeon present within Minas Basin during 2012–2014, including the percentage from the Kennebec (KR) and Saint John River (SJR), and the mean number of days ($\pm$ SD) spent in both locations

| Year	No. of Sturgeon	KR (%)	SJR (%)	Mean No. days
2012	59	32	68	14.6 ± 10.8
2013	50	26	74	6.2 ± 5.8
2014	50	26	74	5.9 ± 5.8

In MB, the average number of co-occurrences was highest in 2012; however, the average SRI was below 0.10 (Table 2; Fig. 3). The low strength of the simple ratio index (SRI) in most years analyzed suggests that Atlantic Sturgeon had a low likelihood of spatio-temporal overlap with others while in the proximity of an acoustic receiver. Excluding 2014 (SRI, Coefficient of Variation (CV) = 5.48, random CV = 5.20, $p = 0.25$), the coefficient of variation was significantly higher than the null networks during 2012 (SRI, CV = 3.05, random CV = 1.77, $p = 1.80 \times 10^{-3}$) and very close to significant during 2013 (SRI CV = 5.68, random CV = 4.30, $p = 0.06$).

### Co-occurrences and Atlantic Sturgeon attributes

More than 50% of dyads detected within MB during 2012–2014 consisted of individuals from the same genetic river of origin. However, most dyads were captured on different days (Table 2). The results from MRQAP-DSP regression indicated that genetic river of origin and initial capture dates were not predictors of the presence of a co-occurrence within MB (Table 3).

Discussion

Atlantic Sturgeon formed co-occurrences within MB that were significantly different than would be observed by chance. Atlantic Sturgeon form large aggregations within feeding locations and this study provided evidence
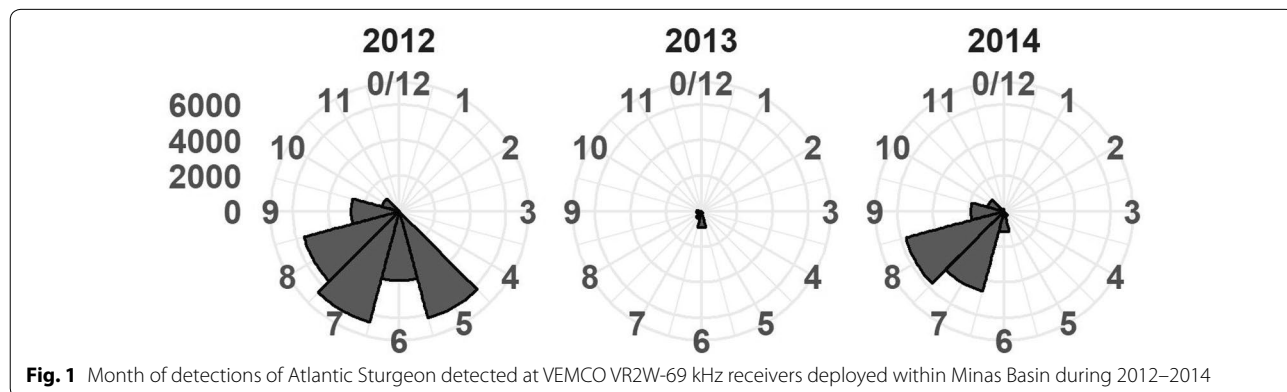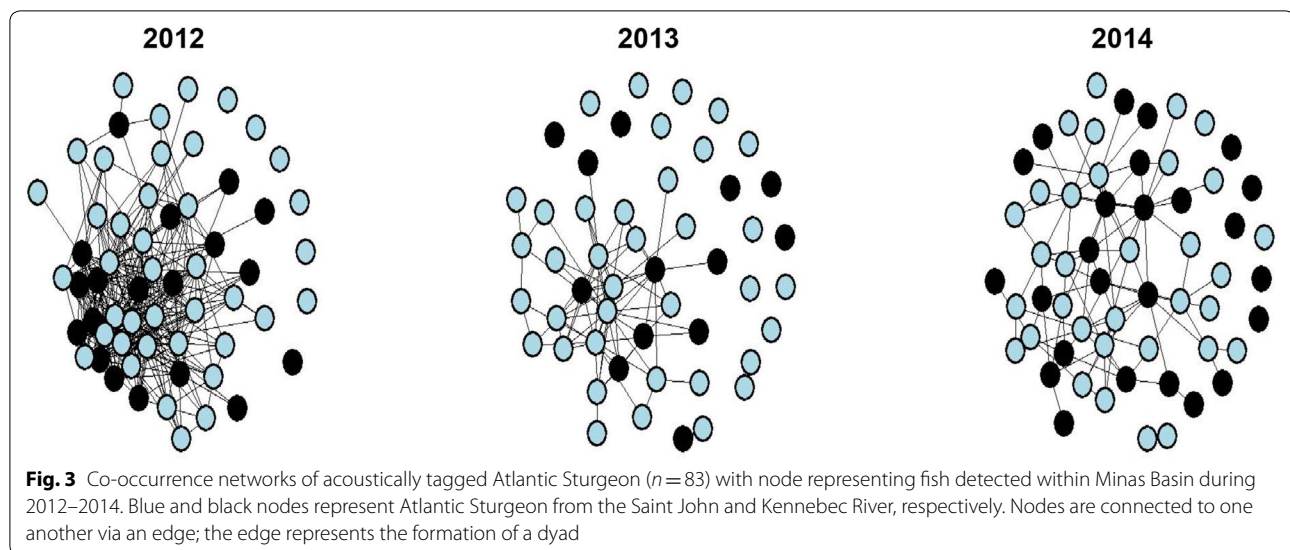

Fig. 1 Month of detections of Atlantic Sturgeon detected at VEMCO VR2W-69 kHz receivers deployed within Minas Basin during 2012–2014

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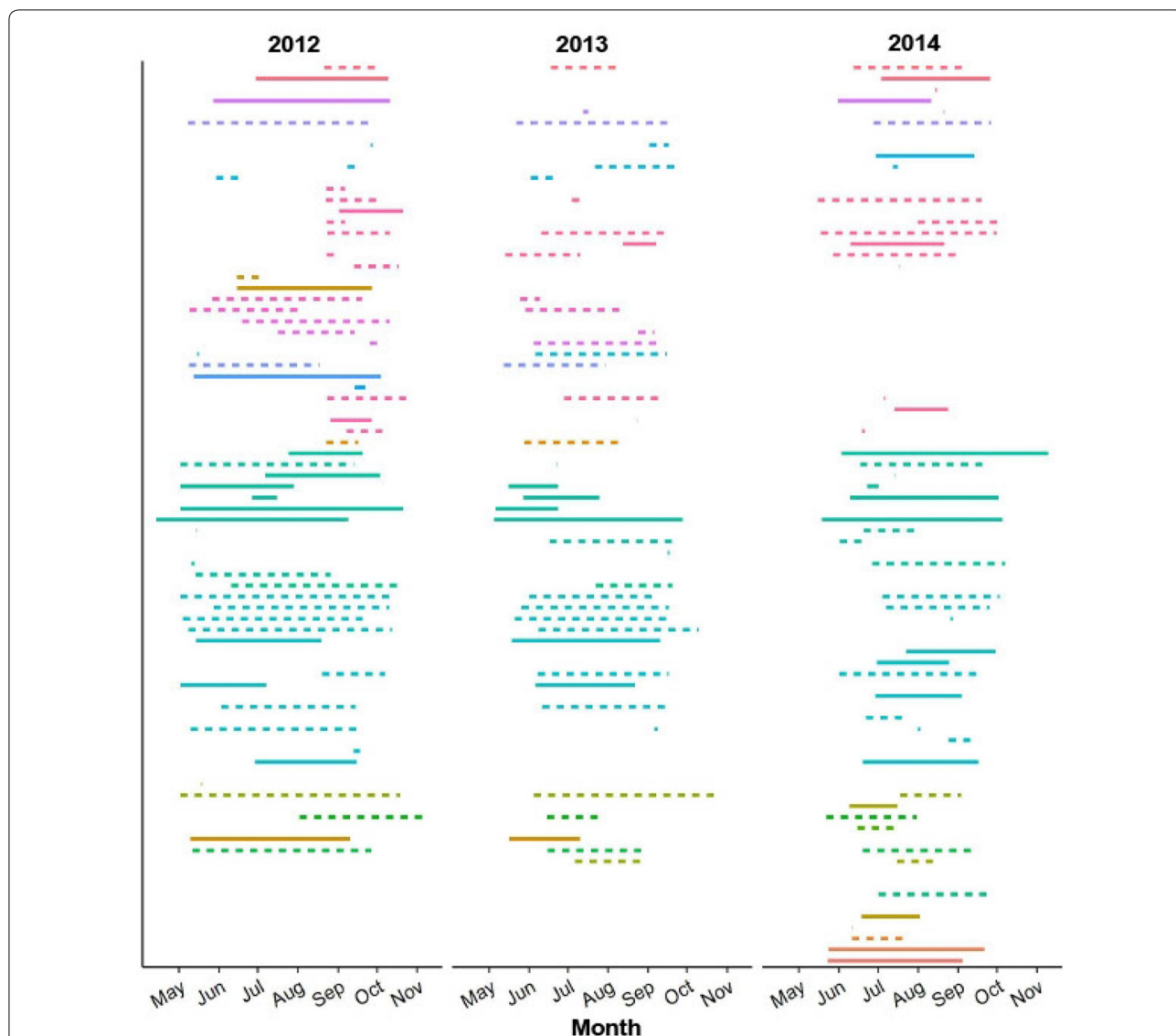
Fig. 2 Time series plot depicting the duration Atlantic Sturgeon (*n* = 83) spent within Minas Basin, Nova Scotia during 2012, 2013, and 2014. Each horizontal line represents a unique Atlantic Sturgeon. The dashed and solid lines represent Atlantic Sturgeon from the Saint John (Canada) and Kennebec River (U.S.), respectively. Colored lines represent unique capture dates of Atlantic Sturgeon

Table 2 Description of dyads detected within Minas Basin during 2012–2014, including the mean (± Standard Deviation; SD) simple ratio index (SRI), the mean (± SD) nodal degree, and the characteristics of the dyads (genetic river of origin and initial capture date)

Year	Location	Mean SRI	Mean degree	Total no. of dyads	Genetic		Capture date	
					% same	% different	% same	% different
2012	MB	0.08 ± 0.08	13.04 ± 8.76	339	55	45	12	88
2013	MB	0.17 ± 0.17	4.47 ± 4.24	76	66	34	12	88
2014	MB	0.15 ± 0.13	3.68 ± 2.92	92	52	48	13	87

Fig. 3 Co-occurrence networks of acoustically tagged Atlantic Sturgeon ($n=83$) with node representing fish detected within Minas Basin during 2012–2014. Blue and black nodes represent Atlantic Sturgeon from the Saint John and Kennebec River, respectively. Nodes are connected to one another via an edge; the edge represents the formation of a dyad

Table 3 Results from MRQAP-DSP regression displaying the effect of genetic river of origin (genetic), and initial capture date (capture) on the presence of co-occurrences of during 2012–2014

Predictor	2012		2013		2014	
	Coefficient	*p*	Coefficient	*p*	Coefficient	*p*
Genetic	-2.0×10^{-4}	0.93	1.2×10^{-3}	0.72	4.1×10^{-3}	0.06
Capture	5.0×10^{-3}	0.93	-4.8×10^{-3}	0.35	2.0×10^{-3}	0.45

All predictors were not significantly correlated with the presence of a co-occurrence during each of the years analyzed. In addition, the variance explained by the models was extremely low (2012: $R^2 = 1.3 \times 10^{-2}$, 2013: $R^2 = 8.5 \times 10^{-4}$, 2014: $R^2 = 2.40 \times 10^{-3}$)

that some Atlantic Sturgeon preferentially co-occur with other individuals. Sturgeons' co-occurrence behavior may be similar to that reported for several species of shark [39–41] which have been thought to undergo solitary marine migrations but preferentially co-occur at feeding sites [5]. Most behavioral studies examining co-occurrence behavior have focused on teleost fishes [6, 10] and may not be directly comparable to more primitive chondrostei such as the Atlantic Sturgeon.

Atlantic Sturgeon co-occurrence

The mean number of co-occurrences between individuals was found to be high within MB. Receivers within MB are located on mudflats where Atlantic Sturgeon aggregate during high tide and retreat during low tide [42]. Despite the highest receiver coverage in MB, 2012 had the greatest number of co-occurrences, but the lowest mean SRI, providing evidence that association strength is weak within MB. In addition, the CV of detected co-occurrences of Atlantic Sturgeon within MB was significantly higher than would be expected by chance during 2012 and very close to significant during 2013, but this was not the case in 2014. In this study, we were only able to describe patterns in co-occurrences between Atlantic

Sturgeon, and unable to characterize social interactions [6]. This is due to the inability to record interactions with acoustic telemetry data since it only provides information regarding when individuals co-occur. However, there is evidence that some individuals may preferentially co-occur which is a requirement for the formation of social groups [5].

Klimley and Holloway [6] noted that if individuals display a tendency for preferential co-occurrences then they should be captured on the same day and return to the same locations successively. Within MB Atlantic Sturgeon were almost equally as likely to form co-occurrences with individuals captured on the same versus different days, or same versus different genetic river of origin. This indicates that Atlantic Sturgeon do not form preferential co-occurrences with individuals that have similar life history characteristics. However, future studies should increase receiver coverage over time and include more tagged individuals, to determine if sturgeon preferentially co-occur with kin or familiar individuals.

Species that exhibit social preferences tend to aggregate with familiar individuals regardless of environmental drivers [15]. The formation of social groups has been more commonly recognized in species that exhibit

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strong site fidelity, such as Blacktip Reef Sharks, *Carcharhinus melanopterus* (Quoy & Gaimard, 1824) and the Spotted Wobbegong Shark (*Orectolobus maculatus*, Bonnaterre, 1788) [4, 15]. Grouping with familiar individuals in dense aggregation regions may help to corral prey and protect against aggression from conspecifics [4, 15]. Mourier et al. [15] noted that Blacktip Reef Sharks displayed some association preferences, exhibiting similar home ranges with individuals of similar size and sex regardless of food resource availability. The Spotted Wobbegong Shark exhibits long term co-occurrences with the same individual, regardless of the presence of high densities of other individuals [4]. A more solitary species, the Sand Tiger Shark (*Carcharias Taurus Rafinesque*, 1810) undergoes solitary marine migrations but aggregates with conspecifics for prolonged periods in ecologically important areas, spending multiple days near specific individuals [40]. However, it is unknown whether these sharks were actively engaging in social preference or just utilizing a food resource [40]. Atlantic Sturgeon also undergo extensive marine migrations and have been known to aggregate with others for prolonged periods at feeding sites, breeding, and overwintering sites [3, 43–45]. Our current study contributed to this body of work by identifying that Atlantic Sturgeon aggregate with conspecifics and that some individuals exhibit preferential co-occurrences.

The formation of preferential co-occurrences exhibited by Atlantic Sturgeon in our study have also been reported in white sharks (*Carcharodon carcharias* Linnaeus, 1758). Schlids et al. [5] noted that white sharks, while known to be solitary, form aggregations within feeding zones such as pinniped colonies. Furthermore, within these feeding zones they exhibit preferential co-occurrences. Unlike teleost species such as the Atlantic Bluefin Tuna (*Thunnus thynnus* Linnaeus, 1758), white sharks have few natural predators and do not require the protection of a shoal of familiar individuals throughout their marine migration [46].

The only known natural predator of Atlantic Sturgeon adults is the white shark, and a small number migrates annually into the Bay of Fundy [46]. The lack of natural predators may explain why these two species undergo solitary marine migrations. Findlay et al. [39] hypothesized that white sharks may aggregate at specific locations due to food availability. Atlantic Sturgeon are also known to aggregate within Minas Basin to feed on benthic polychaetes which are found in high densities [33, 47]. For solitary migratory species, aggregating with familiar individuals within feeding sites may be beneficial to facilitate the transfer of knowledge of foraging strategies, and the location of prey from experienced fishes to naïve individuals.

The finding that Atlantic Sturgeon can form preferential co-occurrences may also be related to sturgeon following a similar migratory route around MB. MP connects MB to the Bay of Fundy, and approximately 14 billion tons of water flows through MP during each flood tide, and the high flow through the MP creates a residual current of 0.8 m/s within MB [48]. The residual current flows around MB in a clockwise direction, and it has been hypothesized that Atlantic Sturgeon follow this current. Future studies should expand the use of SNA within other known feeding, breeding and overwintering sites for Atlantic Sturgeon to determine whether our results may have been an artifact of the current circulation within MB.

This study provided evidence that Atlantic Sturgeon preferentially co-occur with each other when they form feeding aggregations; however, co-occurrences may not be linked to river of origin. This is a particularly important finding for migratory species from populations of varying conservation statuses to help inform management of transboundary species.

Conclusion

Understanding patterns in associative behavior in large free-ranging aquatic fishes, particularly those listed as threatened or endangered, is required to help better inform management decisions. This study indicates that combining SNA and acoustic telemetry data provides the means to assess patterns in spatio-temporal co-occurrence of fishes. The results of this study indicated that Atlantic Sturgeon may actively share time and space within their known summer feeding site located in MB, Nova Scotia. It is currently unknown how Atlantic Sturgeon locate ecologically essential habitats; however, it has been proposed that fishes can engage in social learning [38]. Future studies should expand receiver infrastructure to better characterize migratory patterns of the species and understand co-occurrence behaviors across a broader range of habitats and life-stages.

Methods

Minas Basin (MB)

The Bay of Fundy (BoF) is a region that extends between New Brunswick (NB) and Nova Scotia (NS), Canada. This region has the highest tides in the world, with a maximum amplitude of 17 m in Cobequid Bay [49–51]. The BOF is connected to MB ($\sim 45°27'36'$N, $64°18'12'$W) through MP ($\sim 45°34'82'$N, $64°39'27'$ W); a 5-km-wide, 15-km-long, 150-m-deep channel (Fig. 4) [49]. Tidal current speeds in this region reach up to 6 m/s [52]. MB is a mega-tidal embayment located within NS, Canada, with an area of approximately 115,000 hectares [53]. Due to

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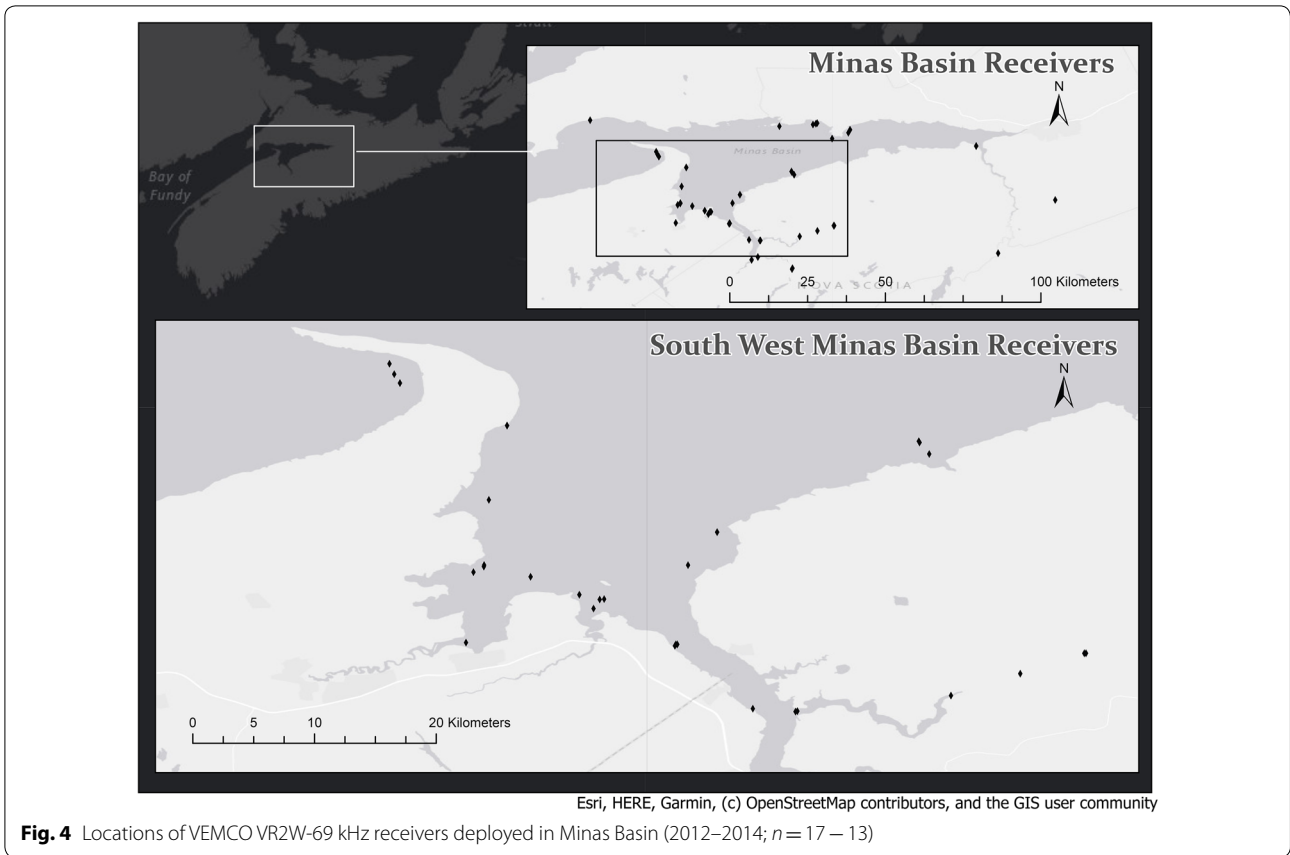
Fig. 4 Locations of VEMCO VR2W-69 kHz receivers deployed in Minas Basin (2012–2014; $n = 17 - 13$)

Table 4 Summary of V16–69 kHz tag types implanted in Atlantic Sturgeon that had genetic assignment during 2010–2014 ($n = 103$)

Year	VEMCO tag type	Number deployed	Battery life (days)	Approx. tag death (yyyy-mm)	Genetic assignment (No. sturgeon)	
					KR	SJR
2010	V16-6x	10	1633	2015-02	4	6
	V16P-6x	10	1287	2014-02	2	8
	V16TP-6x	5	1609	2015-01	1	4
2011	V16P-6x	53	1287	2015-01	26	27
2012	V16P-6x	15	1287/1581	2016-04/2016-12	5	10
2013	–	–	–	–	–	–
2014	V16P-6x	10	2751	2021-12	5	5

Atlantic Sturgeon were not tagged during 2013

the extreme tides in MB, shorelines and sandstone cliffs are eroded, contributing to high turbidity [53, 54].

Atlantic Sturgeon capture and sampling
During 2010 to 2014 Atlantic Sturgeon were captured through directed otter trawl and weir fishing and internally implanted with acoustic tracking tags (Table 4). The trawl consisted of a 24-m box trawl with a 140 mm mesh size and modified rock hopper equipment [31] and trawls ranged between 30 and 60 min. A fishing weir is a large V-shaped net, constructed in the intertidal zone with wings extending up to 1 km and with walls approximately 2.2 m in height [55]. During high tide the walls of the weir are submerged. During ebbing tide, fish are funneled by the walls to a trap located where the two wings merge

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[55]. Atlantic Sturgeon were released from the weirs into a holding pool for sampling.

In 2010 and 2011, Atlantic Sturgeon were captured by research-directed trawl in MB near Cheverie (Fig. 5). In 2012 trawls occurred in the Southern Bight, off Cambridge. In addition, during 2010 and 2011, Atlantic Sturgeon were captured at the Five Islands weir in MB. Atlantic Sturgeon also captured at the Bramber Weir located in the Southern Bight of MB in 2014 (Fig. 5).

Acoustic tagging

Atlantic Sturgeon were measured for fork length (L_F) and total length (L_T; cm), and externally implanted with a FLOY dart tag with a unique number and a return address (Floy Tag & Manufacturing Inc., Seattle, Washington). Floy tags were inserted under the dorsal fin and anchored through the pteriogyte bone [31]. Each Atlantic Sturgeon was internally implanted with a V16–69 kHz VEMCO acoustic tag (Table 4). The V16 tags had an estimated battery life that ranged between 1287 and 2751 days and were set to emit 8 burst pings at 69 kHz with a nominal delay of 75 s. The acoustic power level was set to high (158 dB).

Anesthetic was not used for surgeries as it increases handling time and has been shown to increase postrecovery cortisol levels in Atlantic Sturgeon [56]. For the surgery procedure sturgeon were placed on their dorsal side. The area on their ventral side where the incision occurred was disinfected with 10% Betadine ™ solution

and rinsed with a 0.9% sodium chloride solution [34]. A 30-mm lateral incision was made 40–60 mm anterior to the pelvic fin near the *linea alba* [42, 57]. Sutures were tied in double square knots [57]. All handling and surgical procedures occurred in < 15 min.

All fishing was conducted under the Department of Fisheries and Oceans Scientific License to Fish #322595. Atlantic Sturgeon surgical procedures were performed under Acadia Animal Care Committee protocol #07-11.

Determining life history characteristics
Genetic analysis

Each Atlantic Sturgeon collected from MB was assigned a spawning river of origin using Individual-Based Assignment (IBA) testing implemented in ONCOR [58] as originally described for Atlantic Sturgeon in the BOF in Wirgin et al. [33] and subsequently in Stewart et al. [59] ONCOR assigned individuals in the mixed MB collections to the reference population that would have the highest probability of producing the given genotype in the mixture. ONCOR uses the method of Rannala and Mountain [60] to estimate this probability.

Assignments were based on a combination of microsatellite DNA genotypes at 11 informative loci and mtDNA control region sequencing data. Composite genotypes of MB individuals were compared to those of a reference collection set of 1295 subadult ($\leq$ 50 cm TL) and adult ($\geq$ 130 cm TL) specimens collected from 11 spawning rivers coastwide ranging from the St. Lawrence River,
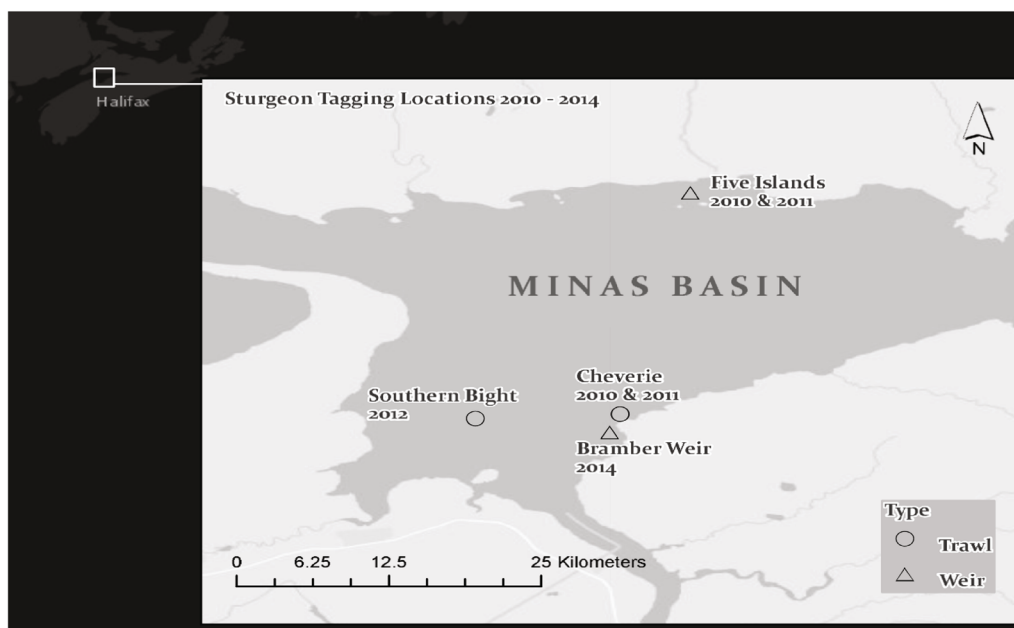
Fig. 5 Locations of research directed otter trawls and weirs used within Minas Basin (MB) for Atlantic Sturgeon capture during 2010–2014

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Quebec, to the Altamaha River, Georgia exactly as described in Stewart et al. [59]. While mean assignment accuracy to individual population coastwide in leave-one-out tests implemented in ONCOR [58] was 85.8%, assignment accuracy to the Saint John River was much higher at 97.8% with most misassignments occurring for the proximal Kennebec River. All DNA was isolated from fin clips that were preserved in 95% ethanol. All genotyping was done at NYUMC laboratory exactly as described in Wirgin et al. [61].

Acoustic receivers

Acoustic tagging data were collected from VR2W-69 kHz receivers in MB during 2012–2014 (Fig. 3, Table 2). Receiver coverage in MB varied by year; however, each year receivers were deployed in areas where Atlantic Sturgeon are known to aggregate in high densities [42]; Fig. 3; Table 5). Range test procedures are described in McLean et al. [42]. The estimated range of VR2W-69 kHz receivers within MB was 500 m.

Analysis of acoustic data
Filtering false detections

Acoustic data were filtered for false detections using the *GLATOS* package [62] in R version 3.5.0 [63]. Detections that did not correspond to any tag ID recognized by VEMCO were removed, and the data were then filtered for Atlantic Sturgeon detections.

The genetic origin of Atlantic Sturgeon detected by the MB receivers during 2012 to 2014 was recoded to values that represented the river of origin of the fish. If an Atlantic Sturgeon individual was not given a genetic assignment, then it was removed from the dataset. Atlantic Sturgeon genetically assigned to the KR were classified as 1 and Atlantic Sturgeon genetically assigned to the SJR were classified as 2.

Social analyses

Our acoustic data at each receiver were represented by $D = \{S_z, t_z, l_z\}_{z=1}^{Z}$, where Z was the total number of Atlantic Sturgeon detected at one acoustic receiver during each year (2012–2014), S_z was equal to the ID code

Table 5 Time periods VEMCO VR2W-69 kHz receivers were deployed within Minas Basin (MB), Nova Scotia during 2012–2014

Receiver location	Months deployed	Approx. range	No. of receivers		
			2012	2013	2014
MB	Apr–Nov	500 m	17	11	13

for one Atlantic Sturgeon, t_z was the time at which an individual sturgeon was detected at a receiver, and l_z was the location of each receiver. Co-occurrences were defined based on the temporal difference in arrival at an acoustic receiver. To define spatio-temporal co-occurrences, the R package *asnipe* [64] was used. Co-occurrences were defined based on the "gambit of the group assumption"—interactions between members of populations are not apparent, and if individuals are in close enough spatiotemporal proximity to one another to interact, then they were assigned to the same group and designated as co-occurring [22, 65, 66]. To ensure that we were able to accurately define the network of Atlantic Sturgeon within MB, we removed data from individuals with less than five detections [15]. This procedure has been used in several SNA studies [5, 39]. Using the "gambit of the group" approach requires defining the spatiotemporal proximity in which individuals could be assumed to be co-occurring [67].

Social network analysis

Associations were defined based on individuals being detected within an 11-h sampling period at a receiver during a 24-h interval. A sampling period is the duration between co-occurrence of two individuals at an acoustic receiver, if two individuals are detected within a sampling period then they are assumed to co-occur [25]. An interval is the time allotted between sampling periods [25]. An interval is used to ensure that co-occurrence strength is not exaggerated and to allow for re-organization of the network [25, 39]. An interval of 1 day was chosen for this study.

Co-occurrences within each study location were defined using the Simple Ratio Index (SRI), and were calculated using the package *asnipe* [64]. Here, the SRI is represented by

$$SRI = \frac{x}{x + y_{AB} + y_A + y_B}$$

where x is the number of sampling periods where co-occurrences are scaled between 0 (never observed in the same group) and 1 (always occurred in the same group). Y_{AB} is the number of sampling periods in which both Atlantic Sturgeon were detected but at different locations, Y_A is the number of sampling periods where only sturgeon A was detected and Y_B is the number of sampling periods where only sturgeon B was detected [68].

The SRI ranges between 0 and 1, where 1 indicates that individuals' strong co-occurrences and values near zero indicate that Atlantic Sturgeon exhibited weak co-occurrences [17, 65]. The SRI was chosen over other indices as acoustic detection data are unlikely to violate the

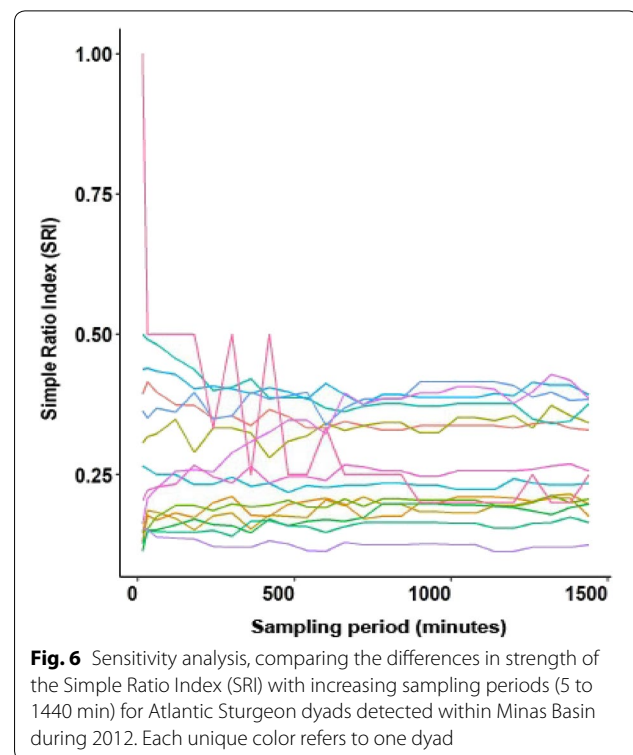Lilly *et al. Anim Biotelemetry*   (2020) 8:14

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assumptions of the SRI. The assumptions state that each individual tracked within the study has an equal opportunity of being detected regardless of whether they formed co-occurrences, and the detection of one individual implies that its associates will also be detected within the sampling period [10, 17]. A concern when using acoustic detection data for SNA is that receivers can have variable detection ranges depending on environmental conditions. Variable detection range may inhibit the assignment of a co-occurrence if one individual is slightly out of range. This study used temporal differences in time stamps that greatly exceeded the tag's nominal delay, decreasing the risk of violating the assumption of equal detection opportunities [10].

Selecting a sampling period

In this study, sampling periods were determined by performing a sensitivity analysis, comparing co-occurrences defined based on temporal differences of 15 min, 30 min and between 1 and 24 h, accounting for 26 calculations of SRIs [4, 39]. Thirty-one pairs of Atlantic Sturgeon (~ 10%) exhibiting the highest co-occurrence strengths from the 15-min network during 2012 were selected for analysis. The SRI fluctuated between 15 min and 11 h (660 min) and then for most dyads stabilized after 11 h (Fig. 6); therefore, an 11-h sampling period was chosen for analysis [4]. Atlantic Sturgeon are known to aggregate at specific locations within MB for multiple days; therefore, it is still likely that they could remain within close spatial–temporal proximity during a sampling period of 11 h (Dr. M. Dadswell, Acadia University, Wolfville, Nova Scotia, oral communication, 2018).

Testing for preferred co-occurrences

To test whether Atlantic Sturgeon form preferred or random co-occurrences within MB, we compared the observed co-occurrence indices to those calculated from permuted networks for each year (2012–2014) [17]. Permutations involved swapping sturgeon between groups at the same receiver location and recalculating the SRI after randomizations [25]. The coefficient of variation (CV) of the SRI from the permuted networks was compared to the observed network, and a *p* value was calculated by determining the total number of times the CV of the observed network was less than the CV of the randomized networks and dividing by the number of permutations ($n = 40,000$) [25]. Forty thousand permutations were used to stabilize the *p* values for data from MB [10]. The population of Atlantic Sturgeon was assumed to exhibit preferred co-occurrences if their CV was greater than the 97.5% of the permuted CVs [39]. Social differentiation (*S*) represents the CV of the observed networks. Due to the high social differentiation (*S*) of the

Fig. 6 Sensitivity analysis, comparing the differences in strength of the Simple Ratio Index (SRI) with increasing sampling periods (5 to 1440 min) for Atlantic Sturgeon dyads detected within Minas Basin during 2012. Each unique color refers to one dyad

observed networks (*S*; 2012–2014: 3.04, 5.68, 5.48), few co-occurrences per individual were required to reject the null hypothesis (*H*; 2012–2014: 7.39, 1.24, 1.79) [69]. Therefore, the power of the permutation tests conducted within MB during 2012–2014 ($S^2 \times H > 5$; 68.30, 7.04, 9.81) was sufficient to test for preferred co-occurrences [69].

Influence of genetic river of origin and capture date on co-occurrence strength

After extracting SRIs, Atlantic Sturgeon co-occurrences detected in MB (2012–2016) were categorized into subgroups consisting of those that had the same genetic river of origin (Kennebec/Kennebec, Saint John/Saint John) and those that had different genetic river of origins (Kennebec/Saint John) and those captured on the same and different days, respectively. Using the double-semi-partitioning technique, Multiple Regression Quadratic Assignment Procedure (MRQAP) was run to determine whether matrices formed based upon the unique characteristics of dyads were predictors of co-occurrence strength within MB [70, 71]. MRQAP was run with 20,000 permutations and the partial correlation coefficients of each predictor variable were extracted [70, 71]. The predictor matrices (genetic river of origin, capture date) were assessed for collinearity using Mantels tests (10,000 permutations) prior to analysis using the R package vegan [72].

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