

**THE SOCIALITY OF ATLANTIC STURGEON AND SAND TIGERS IN AN  
ESTUARINE ENVIRONMENT**

by

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A thesis submitted to the Faculty of the University of Delaware in partial  
fulfillment of the requirements for the degree of Master of Science in Marine Studies

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## TABLE OF CONTENTS

LIST OF TABLES .....	v
LIST OF FIGURES .....	vi
ABSTRACT .....	vii
Chapter	
1 INTRODUCTION .....	1
2 METHODS .....	7
Data Collection .....	7
Social Network Metrics .....	9
Environmental Conditions and Hourly Social Networks .....	12
Social Network Analysis .....	13
3 RESULTS .....	16
Environmental Conditions .....	16
Sampling Period .....	17
Social Network Analysis .....	19
4 DISUSSION .....	22
REFERENCES .....	29
Appendix	
SUPPLEMENTARY MATERIALS .....	39

## LIST OF TABLES

Table 1	Numbers of Atlantic sturgeon (AS) and sand tiger (ST) within the 2012 networks. The AS and ST networks began on 21 Mar and 19 Apr respectively and ended on 24 Nov and 28 Oct 2012. Individuals are separated by sex, maturity, and natal spawning river.....	8
Table 2	Numbers of Atlantic Sturgeon (AS) from each natal spawning river. ....	9
Table 3	Observed (Obs.) network coefficient of variation (CV), modularity (Q) and assortment (AST) with standard error and P-values (p) for maturity (M), sex (S), and river (R) for Atlantic sturgeon (AS), sand tigers (ST), and the mixed species (SP) networks. ....	19
Table 4	Linear regressions estimated (Est.) the impact of environmental variables (retriever from NOAA’s Brandywine Shoal Light (Station ID: 8555889) on detection frequency of Atlantic sturgeon and (AS) sand tigers (ST) (June 9th - October 7th, 2012). Significant negative correlations were found between hourly measurements of change in tidal height (CTH) and wind stress (WS) and the number of detections per receiver. CTH was measured as the first derivative of hourly tidal height measurements (m) and wind stress as the wind speed squared (m/s) <sup>2</sup> . The goodness-of-fit for these models is indicated by adjusted R <sup>2</sup> . ....	39

## LIST OF FIGURES

Figure 1	Acoustic receiver locations (n =73) from 2012, within the Delaware Bay and surrounding coastlines.....	7
Figure 2	Spectral analysis of hourly environmental variables and network metrics (June 9th - October 7th, 2012) for A-B) Atlantic sturgeon and C-D) sand tigers. 2 Columns .....	17
Figure 3	Sensitivity analysis of A) Atlantic sturgeon and B) sand tiger SRI strengths for sampling periods of 6 hours, 12 hours and 1-30 days. Individual lines represent the SRI of 20 pairs of strongly associated fish. Separate line types and colors are used to identify individual association weights (dyads).....	18
Figure 4	Social Networks of A) Atlantic sturgeons and B) sand tigers in 2012. Nodes are colored by walktrap community placement. The size of each node (AS = 146: ST = 201) represents the proportion of time that individual was detected within that network. Dyad (AS = 946: ST = 9,618) width represents association strength.....	20
Figure 5	Social Network of Atlantic sturgeons and sand tigers in 2012. Nodes are colored by species. The size of each node represents the proportion of time that individual was detected within that network. Dyad (n = 11,268) width represents association strength.....	21
Figure 6	Video of sand tiger movement in the study site from 2012-05-14 to 2012-10-14. Individuals are colored by their maturity state. Video generated with the R package moveVis (Schwalb-Willmann et al. 2020). To watch the video online, please visit <a href="https://www.youtube.com/watch?v=FuU-TqRozS4">https://www.youtube.com/watch?v=FuU-TqRozS4</a> .....	40
Figure 7	Figure.6) Video of sand tiger movement in the study site from 2012-04-19 to 2012-10-15. Individuals are colored by their community as identified by the walktrap algorithm. Video generated with the R package moveVis (Schwalb-Willmann et al. 2020). <a href="https://www.youtube.com/watch?v=lvq2JuaT0mM">https://www.youtube.com/watch?v=lvq2JuaT0mM</a> .....	41
Figure 8	Video of Atlantic sturgeon (AS) and sand tiger movement in the study site from 2012-03-21 to 2012-11-23. Video generated with the R package moveVis (Schwalb-Willmann et al. 2020). To watch the video online, please visit <a href="https://www.youtube.com/watch?v=i7c8j1T-TJo">https://www.youtube.com/watch?v=i7c8j1T-TJo</a> .....	42

## ABSTRACT

Social network analyses are used by ecologists to examine the various drivers and functions of animal social structures. While social behaviors are found throughout the animal kingdom their roles in structuring marine communities are poorly understood. In addition, comparisons of sociality across marine fishes in the same location and time are rare. A well-maintained acoustic telemetry network in Delaware Bay allowed me to analyze the sociality of Atlantic sturgeon (*Acipenser oxyrinchus oxyrinchus*) and sand tigers (*Carcharias taurus*). Both species co-occur in the bay, are long-lived, make seasonal migrations, and aggregate for unknown reasons. However, these species occupy distinctly different trophic positions and ecological niches. I found little evidence for sociality amongst Atlantic sturgeon. However, sand tigers exhibited evidence for both preferential co-occurrence and assortment by maturity. In addition, I demonstrate that these species preferentially associate by conspecifics. My findings suggest that sand tigers exhibit a higher degree of sociality than Atlantic sturgeon while in the Delaware Bay. From these findings, I outline the social structures of two evolutionary distinct species while they co-occur in the Delaware Bay. Additionally, I explored the influence that environmental acoustic conditions have on social network metrics and make recommendations for future analyses using acoustic telemetry in estuarine environments.

## **Chapter 1**

### **INTRODUCTION**

Sociality describes cooperative behavior amongst individuals and is common throughout the animals (Tinbergen, 2013). Studies of animal sociality have given particular attention to the influences of social structures such as group living on a population's fitness and survival (Krause et al., 2002; Lehmann et al., 2016). Using social network analysis (SNA), ecologists analyze the costs and benefits of social behaviors by modeling sociality at the individual, pair, group, and population levels (Krause et al., 2009). These tiered analyses allow investigations of the drivers of animal interactions and their consequences on population structure and fitness (Farine and Whitehead, 2015; Krauss et al., 2009). For example, the cost and spread of disease are, in part, determined by the interactions of a population's members (Sah et al., 2018), while an individual's behavioral traits and the strength of their associations within a group can be predictors of survival (Lehmann et al., 2016).

Within fishes, social behavior is often expressed through the formation of aggregations, schools, and preferred associations (Haulsee et al., 2016; Kasumyan & Pavlov et al., 2018; Parrish et al., 2002). While there are many examples of fish aggregations, spatiotemporal proximity does not necessarily indicate the existence of social behaviors. Like the attraction of insects to light, animals may congregate in high density without an intrinsic social interest (Tinbergen, 2013). Applying SNA to occurrence data provides insight into whether the associations are random or the result of an underlying social preference (Farine et al., 2015; Farine, 2017). Thus, SNAs

elucidate a variety of non-random social structures, including preferential and avoided association between individuals and the formation of subgroups (communities) within populations (Anderson et al., 2021; Armansin, 2016; Mourier et al., 2012; Stehfest et al., 2013).

Research on animal sociality has historically focused on terrestrial systems (Jacoby et al., 2016; Mourier et al., 2017) due to the comparative difficulty of working in aquatic environments. The application of SNA to aquatic environments has prompted discussion on the best tools and analytical approaches for generating robust social networks of marine taxa (Mourier et al., 2017). The SNA data collection for marine fishes is limited to either direct observations (Findlay et al., 2016) or acoustic telemetry systems (Armansin, 2016; Jacoby et al., 2016; Papastamatiou, 2020). Acoustic telemetry commonly uses arrays of stationary acoustic receivers to log individually coded transmissions from acoustically tagged animals. Acoustic telemetry systems provide occurrence data that would otherwise be unavailable in aquatic environments where direct observations are impractical. As a result, it is one of the most commonly used approaches in SNA (Anderson et al., 2021; Lilly et al., 2020; Mourier et al., 2017).

Because changing environmental conditions can impact the acoustic environment in marine systems, environmental variables have the potential to impact social networks based on acoustic telemetry (Reubens et al. 2019). Thus, the probability of a tagged animal being detected by an acoustic receiver will change with variations in the environment, with the probability decreasing in acoustically noisy conditions which reduce the range of reception of acoustic receivers (Gjelland & Hedger, 2013; Kessel et al., 2014; Reubens et al., 2019). Variation in wind speed,

water velocity, and depth, amongst other environmental variables, influence sound propagation through water and may impose limitations upon the potential detection range of receivers (Gjelland & Hedger, 2013; Kessel et al., 2014; Reubens et al., 2019). Prior research found that various network properties are altered by the detection ranges inherent to the receivers (Mourier et al., 2017). Therefore, dynamic acoustic conditions should influence the generation of SNA metrics. Comparing aquatic network metrics between locations and study populations remains an intrinsic difficulty of SNA (Farine and Whitehead, 2015), and can be achieved only after carefully considering data collection methods (Bond et al., 2021) and acoustic conditions.

An extensive passive acoustic telemetry receiver array in Delaware Bay, USA, collected occurrence data for two species of large, aggregatory fishes (Atlantic sturgeon, *Acipenser oxyrinchus oxyrinchus*; Sand tigers, *Carcharias taurus*), providing the opportunity to test for sociality in two trophically distinct but co-occurring species. Atlantic Sturgeon are a long-lived, anadromous fish found along the Eastern Seaboard of Canada and the United States (Smith., 1985). Sturgeon primarily consume polychaetes and other invertebrates (McLean et al, 2013). Atlantic sturgeons are predominantly benthic foragers and utilize the olfactory system as the primary foraging sense. Following the identification of a potential food item, they employ the gustatory and electroreception senses (Boglione et al., 2006). Atlantic sturgeon were a species of economic significance and a target of commercial fishing efforts (Smith, 1985) until overexploitation and habitat degradation diminished stocks across the species' range (Borodin 1925, Smith & Clugston, 1997). In 2012, under the US Endangered Species Act, the National Marine Fisheries Service (NMFS) categorized

the Carolina, Chesapeake Bay, New York Bight, and South Atlantic populations as endangered (Federal Register, 2012). As an anadromous species, most research has focused on Atlantic sturgeon migration and spawning behavior. Knowledge of aggregations are generally limited to regions near the mouth of large rivers. (Dunton et al., 2015; Laney et al., 2007; Taylor et al., 2016). These aggregations can be composed of fish from multiple natal spawning rivers (Wirgin et al., 2012; Wirgin et al 2015 a b). An SNA analysis for Atlantic Sturgeon found preferential co-occurrence in one out of three study years, and that natal-spawning river was not a predictor of these preferences (Lilly et al., 2020). Additionally, McLean et al., (2014) hypothesized the movement of Atlantic sturgeon to be associated with tidal foraging opportunities. Breece et al., (2018 a) showed that environmental variables play a key role in mediating movement and residency behaviors in Atlantic sturgeon. Therefore, it is unknown whether these aggregations are driven by social behavior or uncoordinated responses to environmental conditions, or an amalgam of both.

Sand tigers (*Carcharias taurus*) are sharks found throughout much of the world's tropical and warm temperate oceans (Compagno, 2001). Sand tigers have small eyes and a relatively large number of electro sensory pores (Carrier et al., 2010). Therefore, it is likely that the species hunts by electroreception, primarily feeding on teleosts and other elasmobranchs (Carrier et al., 2010; Gelsleichter et al., 1999). Low fecundity and late maturity (Gilmore, 1983; Goldman et al., 2006) make the species vulnerable to overfishing (NMFS, 2009). As a result, NOAA has listed the sand tiger shark as a Species of Concern (Carlson et al., 2009) and the Delaware Bay as a habitat area of particular concern (HAPC) (Rauch, 2017). Sand tigers make seasonal migrations from lower to the Delaware Bay, where they are known to form

aggregations (Rauch, 2017). In addition, sand tigers are reported to use distinct seasonal migration routes determined by sex and size class and to exhibit coordinated breeding behaviors (Gilmore et al., 1983; Gilmore, 1993; Haulsee et al., 2016; Kneebone et al., 2014; Teter et al., 2015). In 2016, a sand tiger SNA provided evidence for the first observed case of fission-fusion behavior (changes in group size and composition related to behavioral modes; summering, south migration, community bottleneck, dispersal, north migration) observed in elasmobranch (Haulsee et al., 2016), indicating that they may be exhibiting sociality at finer scales than previously observed.

Despite the varied ecologies and life histories of these two species both are known to form seasonal aggregations within the Delaware Bay for unknown reasons (Breece et al., 2016, 2018 b; Rauch, 2017). This sets up an interesting comparison of social behavior between two distantly related species (evolutionarily diverging ~ 465 MYA), which spend significant time in the Delaware Bay during the spring and summer (Kumar et al., 2017). The Delaware Bay is situated on the mid-Atlantic Seaboard of the United States. As a relatively shallow water estuary, it is suitable for the deployment of and recovery of passive acoustic telemetry arrays (Kilfoil, 2014).

Here, I investigate the sociality of Atlantic sturgeons and sand tigers in the Delaware Bay. I use acoustic telemetry to generate multiple network metrics, reviewing the extent of social interactions at the pair, community, and population level. Because fluctuating environmental conditions may influence the detectability of these species, I also investigate the influence of dynamic acoustic conditions on the generation of network metrics. This research builds on our fundamental understanding

of the structure of marine fish aggregations, and tests for differences in potential sociality in trophically distinct, but co-occurring species.

## Chapter 2

### METHODS

#### Data Collection

The Delaware Bay is a coastal estuary situated mid-way along the eastern seaboard of the United States. The bay is dominated by freshwater input from the Delaware river and a semi-diurnal tidal regime, resulting in a 120 km long salinity gradient (Sharp, 2010). In 2012, an array of passive acoustic receivers (n = 73, VR2, and VR2W; VEMCO Ltd.) recorded the occurrence of tagged fish within the Delaware Bay and surrounding coastal waters (Figure 1). Although acoustic detection

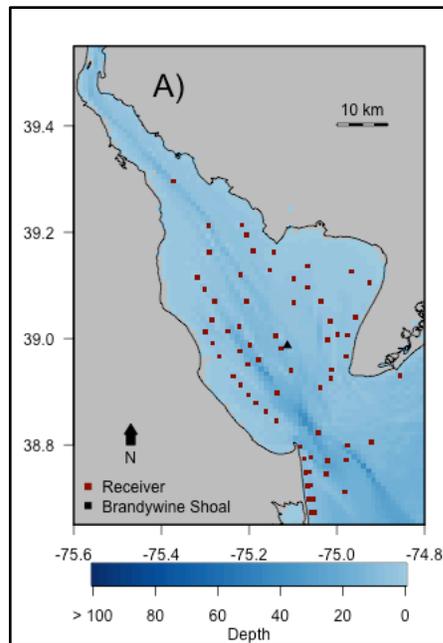


Figure 1 Acoustic receiver locations (n =73) from 2012, within the Delaware Bay and surrounding coastlines.

range is highly variable (Reubens et al., 2019), the maximum detection range of acoustic arrays within the study area is typically between 600-1000m (Kilfoil, 2014). Additionally, Oliver et al., (2017) and Haulsee et al., (2015) found detection frequency to be below 10% at distances greater than 600 m and 750 m respectively in the Mid-Atlantic Bight’s coastal waters. From 2008 to 2013, a collaborative effort led by Delaware State University tagged Atlantic sturgeon (n = 181) and sand tigers (n = 207) (See Table 1). Captured individual were surgically implanted with internal

Table 1 Numbers of Atlantic sturgeon (AS) and sand tiger (ST) within the 2012 networks. The AS and ST networks began on 21 Mar and 19 Apr respectively and ended on 24 Nov and 28 Oct 2012. Individuals are separated by sex, maturity, and natal spawning river.

	AS	ST
Immature	29	56
Mature	117	145
Male	22	110
Female	39	91
Unknown Sex	85	--
Total	146	201

acoustic transmitters (V16-6 h 69 khz; battery life ~ 6.4 yr; mean transmission rate ~ 90s VEMCO LTD Bedford, NS, Canada) (Breece et al., 2016, 2018 a; Haulsee et al. 2015, 2016). The handling protocol, ethics statements, and sampling methods are found in Breece et al., (2018 a,b), Fox et al., (2000), and Haulsee et al. (2016). The maturity state of captured fish was estimated from total length using growth curves (Goldman et al., 2006; Dunton et al., 2016). In sturgeon, both sexes were considered

mature at 150 cm (Dunton et al., 2016; Van Eenennaam et al., 1996), and in sand tigers 220 cm and 190 cm for females and males respectively (Gilmore et al., 1983). The sex of sand tigers was identified for all individuals by observing the presence or absence of claspers. When possible, the sex of Atlantic sturgeon was determined by internal gonad sample (Breece et al., 2018 b), thus sturgeon sexes are placed into one of three categories; “female”, “male”, and “unknown”. (Table 2). A fin clip was taken from Atlantic sturgeon to determine natal spawning river by mitochondrial DNA control region sequencing (Wigin et al., 2015 a,b).

Table 2 Numbers of Atlantic Sturgeon (AS) from each natal spawning river.

	Number of AS
Albemarle R.	8
Altamaha R.	1
Delaware R.	23
Hudson R.	49
James R.	34
Kennebec R.	4
Ogeechee R.	14
Savannah R.	10
St. John R.	3
Total	146

### Social Network Metrics

While active tagging projects were on-going between 2008-2013, I focused this study on the summer season in 2012 when receiver coverage and number of active tags in both species were highest in this region. To determine sociality, SNAs were

generated from the first to last occurrence of Atlantic sturgeon (19 Mar – 24 Nov) and sand tigers (19 Apr – 28 Oct). Associations between individuals (dyads) were determined using the gambit-of-the-group approach (Franks et al., 2010; Whitehead & Default, 1999). I defined a dyad as two tagged individuals recorded at the same receiver within a synchronized ten-minute window (Leu et al., 2016; Farine, 2017; Mourier et al., 2017). This window accounts for the transmitters ~90 s transmission rate, allowing for multiple cycles and increasing the probability of detection and is in congruence with previous studies.

The fundamental unit of animal social networks is the association strength, which measures the proportion of time two animals are in association and was calculated using the Simple Ratio Index (SRI):

$$\text{SRI} = \frac{X}{X+Y_{ab}+Y_a+Y_b} \quad (1)$$

where the number of sampling periods fish “a” and “b” co-occurred ( $X$ ), is divided by the sum of  $X$ , the number of sampling periods both fish were identified but did not co-occur ( $Y_{ab}$ ), the number of sampling periods fish “a” occurred without “b” ( $Y_a$ ), and the number of sampling periods “b” occurred without “a” ( $Y_b$ ) (Farine & Whitehead, 2015). Association strengths range between 0 (two individuals never forming a group) and 1 (two individuals always in the same group) (Farine & Whitehead, 2015). Association strengths between rarely observed individuals can be inaccurate (Farine & Whitehead, 2015), therefore fish with less than five detections per year were removed to ensure network accuracy (Findlay et al., 2016; Lilly et al., 2020; Mourier et al., 2012; Schilds et al., 2019).

The presence of preferred and avoided relationships within social networks can be determined using the coefficient of variation ( $CV$ ) of the association strengths (Farine and Whitehead, 2015). Individuals that preferentially co-occur are expected to have higher association strengths than random, while preferential avoidance would result in lower association strengths. Thus, populations exhibiting preferential co-occurrence or avoidance behaviors are expected to have a higher  $CV$  of association strengths than the permuted networks (Farine & Whitehead, 2015).

To detect clusters within a population, I implemented a cluster walktrap algorithm which was selected over other community detection methods due to its quality of performance and reliability over varying network sizes (Pons & Latapy, 2005). Modularity ( $Q$ ) then determined the association between communities detected by the walktrap algorithm within the entire network.  $Q$  ranges between 0 and 1. A network with a high  $Q$  value has a large proportion of dyads within a community, and few between different communities (Clauset et al., 2004; Newman & Girvan, 2004; Sosa et al., 2020). Following the simulations of Shizuka & Farine, 2016, only  $Q > 0.5$  provide robust evidence for the presence of community structures.

The assortment of each social network was calculated using the R package “assortnet” (Farine, 2014). Assortment measures association bias of individuals by maturity, species, and sex for both populations, and by natal spawning river for Atlantic sturgeon (Farine, 2014). Assortment values range between -1 (disassortment: individuals of different types are more likely to be associated) and 1 (assortment: individuals of the same type are more likely to be associated) (Farine, 2014). The standard error of the assortment values was calculated via the jackknife function in

“assortnet”. When calculating sex assortment, sturgeons of unknown sex were removed from the analysis.

All analyses were conducted using R version 3.6 (R core team, 2019) and SNA were produced using the R packages “asnipe”, “igraph”, and “spatsoc” (Csardi & Nepusz, 2006; Farine, 2013; Robitaille et al., 2019).

### **Environmental Conditions and Hourly Social Networks**

Spectral analyses elucidated the relationship between environmental variables, detections per receiver, and derived network metrics ( $CV$ ,  $Q$ , mean community size, number of communities). This analysis was done from 9 June – 7 Oct, 2012, which represent a time period when Atlantic sturgeons and sand tigers co-occurred in relatively high numbers in the study site. Previous studies have tested the influence of wind and tidal height on the detection range of acoustic receivers (Kessel et al., 2014; Reubens et al., 2019), therefore hourly measurements of wind speed and tidal height were retrieved from NOAA’s Brandywine Shoal Light (Station ID: 8555889) (NOAA, 2020) (Figure 1). From these data, a time series was generated of wind stress, tidal height, and the change in tidal height (as a proxy for water velocity in estuarine environments).

Hourly social network metrics of both species were generated from acoustic telemetry observations. The number of detections per receiver and network metrics of  $CV$ , total number of communities, mean community size, and  $Q$  were calculated for each hourly network. The periodic signal strength of the three environmental variables, four network metrics, and detection per receiver were then compared for one-hour fixed frequencies between 4 and 45 hours. Overlapping frequency signals between environmental variables and network metrics may suggest an environmental

influence on the generation of SNA. All spectra were normalized between 0 and 1 for plotting purposes. Results from this analysis were taken into considerations when selecting the social network analysis' sampling period. Additionally, a series of linear regressions were performed to find the relationship between the environment and detection frequency. These regressions estimated the effects of both the change in water height and wind stress (square of the wind speed) on the number of detections per receiver per hour. To meet the assumptions of normality, the common logarithm was applied to the number of detections per receiver.

### **Social Network Analysis**

Sociality was examined by generating observed network graphs and their respective permuted null models. Atlantic sturgeon and sand tiger networks began on 21 Mar and 19 Apr respectively and ended on 24 Nov and 28 Oct 2012. Creating networks for the entire seasonal occurrence of each species accounts for potential biases that may be introduced from changing environmental conditions revealed by the spectral analysis. These networks calculated the observed value and permuted significance for the metrics of  $CV$ ,  $Q$ , and intraspecies assortment (sex, maturity, and natal spawning river [sturgeon only]). Interspecies assortment was determined by a mixed-species network, including the detections of both Atlantic sturgeon and sand tigers. Each network incorporated data from the first to the last occurrence in the acoustic array. The association sampling periods form the primary temporal unit of social networks by dividing the occurrence data into smaller timeframes (Whitehead, 2008). Too short of an association sampling period may limit the quantity of data available, while too long of a period may lead to a loss of information (Whitehead,

2008). To avoid this, the sampling period of both species was selected by sensitivity analysis (Armansin et al., 2016 & Lilly et al., 2020). In this analysis, the SRI of 20 pairs of fish with the strongest association weights, was recorded for sampling periods of .25, .5, and 1 to 30 days (32 total). A 24-hour interval was used between sampling periods to separate observations (Armansin et al., 2016).

The statistical significance of the observed network metrics was determined by comparing them to permuted null models (Farine, 2017; Farine and Carter, 2021). For  $CV$  and  $Q$ , a null model of conservative pre-network permutations (swapping dyads between fish observed at the same receiver and sampling period) (Farine, 2014 & 2017). The statistical significance of these metrics was then determined by the number of times the permuted value was larger than the observed value, divided by the total number of network permutations. For assortment, permutations were generated using the double permutation method, with the additional step of normalizing the deviation score between 0 and 1 (Farine and Carter, 2021). The double permutation method combines both the conservative pre-network permutations (swapping between location and sampling period) and node permutations, the latter of which randomizes node identity (sex, species, maturity, natal spawning river [Sturgeon only]) (Farine, 2017; Farine and Carter, 2021). Assortment significance was then determined by the number of permuted assortment values greater than the observed, and disassortment as the number of permuted values that were more negative than the observed (Farine, 2014). To ensure  $P$ -value stabilization, 100,000 network permutations were produced for each of the species-exclusive networks and 50,000 permutations for the mixed-species network (Bejder et al., 1998). At no point in the analysis were the observed

metric values directly compared between networks or species (Bond et al., 2021; Farine, and Whitehead, 2015).

## Chapter 3

### RESULTS

#### Environmental Conditions

Spectral analysis revealed overlap in periodicity between environmental variables, detections per receiver, and network metrics at frequencies of  $6.2 \pm 0.2$  and  $12.4 \pm 0.2$  hours (Figure 2), which may reflect sea breeze (12 hr) and tidal frequencies (6, 12 hr). Signals at these frequencies are also present in the detection per receiver and network metrics of both species (Figure 2). In the Atlantic sturgeon spectral analysis (Figure 2 A & B), the signals of wind stress and tidal height are shared by strong and maximum signals of detections per receiver, CV, the number of communities, mean community size, and Q. The change in tidal height frequency overlaps signals in CV and Q. Similar patterns are found with sand tigers derived network metrics (Figure 2 C & D). The wind stress and tidal height frequencies are associated with strong detections per receiver and Q in sand tigers and the tidal height frequencies are coincident with strong signals of detections per receiver, CV, and Q. The linear regressions revealed significant, but weak relationship between detections per receiver per hour and change in tidal height and wind stress (See Appendix A). The number of detections per receiver of both species decreased as both wind stress and the change in tidal height increased (See Appendix A).

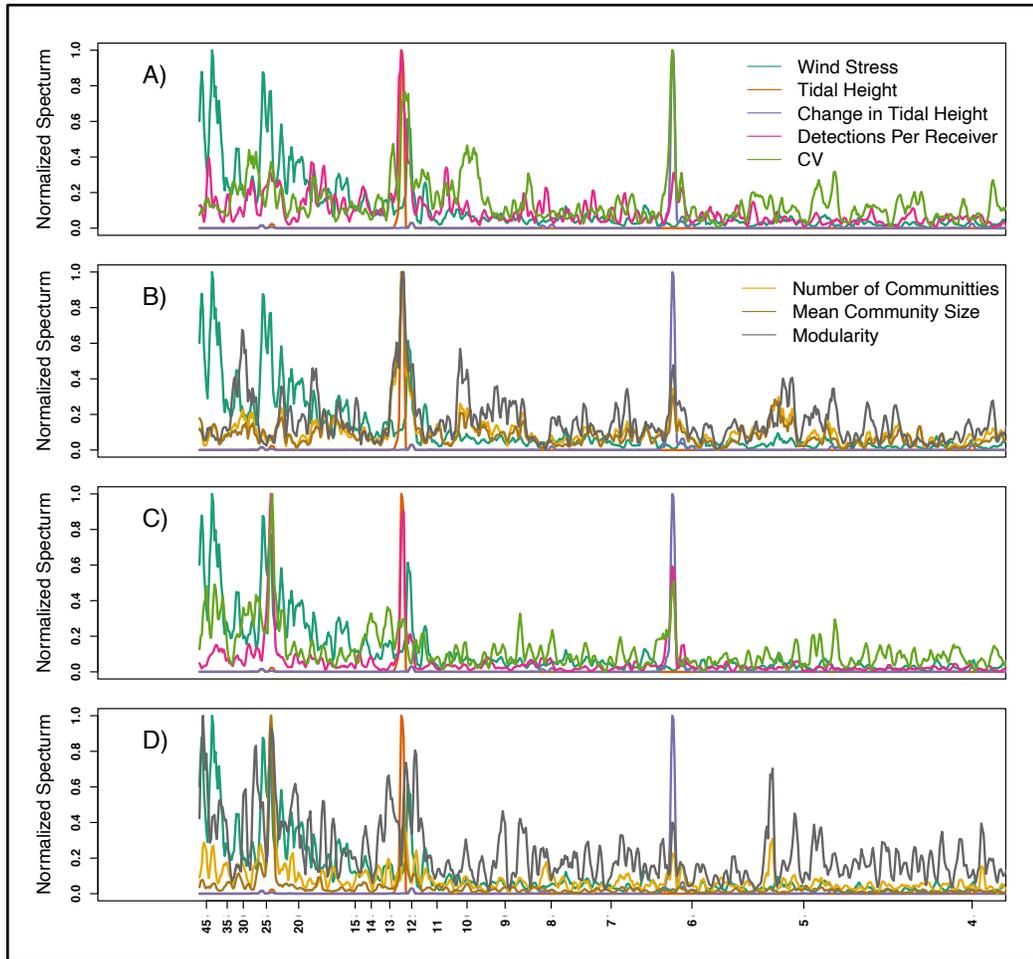


Figure 2 Spectral analysis of hourly environmental variables and network metrics (June 9th - October 7th, 2012) for A-B) Atlantic sturgeon and C-D) sand tigers. 2 Columns

### Sampling Period

Both species showed similar patterns of SRI stabilization, allowing for the selection of an appropriate sampling period for the creation of network graphs. The SRI values of 20 Atlantic sturgeon dyads inclined only slightly or not at all for the first ten sampling periods (Figure 3). For the remaining sampling periods (9-30 days), the SRI values oscillate around a constant value. Conversely, the value of the sand tiger

dyads increased rapidly for the first ten sampling periods. For the remaining sampling periods, they followed a similar pattern of oscillation as documented with Atlantic sturgeons. Thus, a nine-day sampling period was selected for generating yearly social networks of both Atlantic sturgeon and sand tigers (Armansin et al., 2016 & Lilly et al., 2020). It is important to note that the impact of acoustic conditions occurs on much shorter periods (6-24 hours; Figure 2) than the nine-day sampling period selected for the remaining analyses. This reduces the impact of variable acoustic conditions on SNA metric generation, by sampling association strengths over periods greater than the predominant environmental variations.

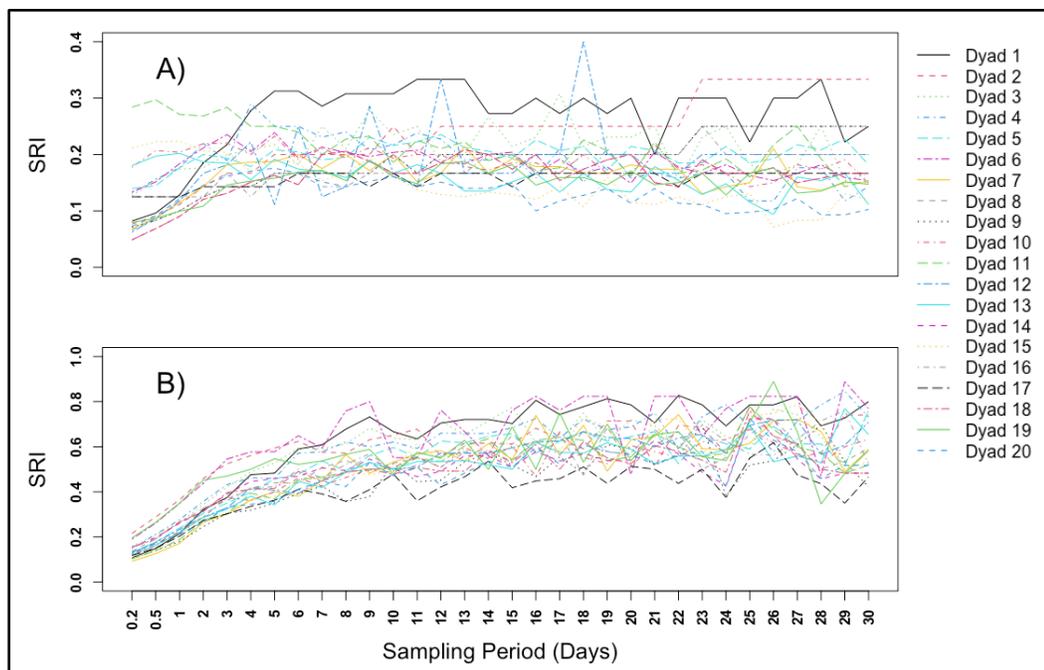


Figure 3 Sensitivity analysis of A) Atlantic sturgeon and B) sand tiger SRI strengths for sampling periods of 6 hours, 12 hours and 1-30 days. Individual lines represent the SRI of 20 pairs of strongly associated fish. Separate line types and colors are used to identify individual association weights (dyads).

### Social Network Analysis

The coefficient of variation of the observed Atlantic sturgeon network was not significantly greater than the permuted null models ( $P = 0.153$ ). Conversely, the coefficient of variation was significant for sand tiger networks ( $CV = 3.855$ ,  $P < 0.001$ ) (Table 3). This suggests that sand tigers, but not Atlantic sturgeon exhibit preferential co-occurrence and avoidance between individuals.

Table 3 Observed (Obs.) network coefficient of variation (CV), modularity (Q) and assortment (AST) with standard error and P-values (p) for maturity (M), sex (S), and river (R) for Atlantic sturgeon (AS), sand tigers (ST), and the mixed species (SP) networks.

	AS	ST	MS
Obs. CV	6.069 (P = 0.153)	3.855 (P = <0.001)	--
Obs. Q	0.467 (P = 0.252)	0.425 (P = 0.003)	--
Obs. M-AST	0.118±0.079 (P = 0.247)	0.143±0.049 (P = 0.003)	--
Obs. S-AST	-0.081±0.085 (P = 0.597)	0.014±0.020 (P = 0.694)	--
Obs. R-AST	-0.022±0.016 (P = 0.258)	--	--
Obs. SP-AST	--	--	<b>0.034±0.021 (P = 0.032)</b>

The modularity of Atlantic sturgeon was not significantly higher than the null model ( $P = 0.113$ ). However, the modularity of sand tiger networks was significantly larger than the permuted null models ( $Q = 0.425$ ,  $P < 0.003$ , Table 3). Sand tigers appear to have stronger community structure than Atlantic sturgeon, however neither species network produced strong Q values ( $Q > 0.5$ ), therefore it is unlikely robust

community structures for either of these species exist within the Delaware Bay (Figure 4) at least on the spatial temporal scales examined here (Shizuka and Farine, 2016).

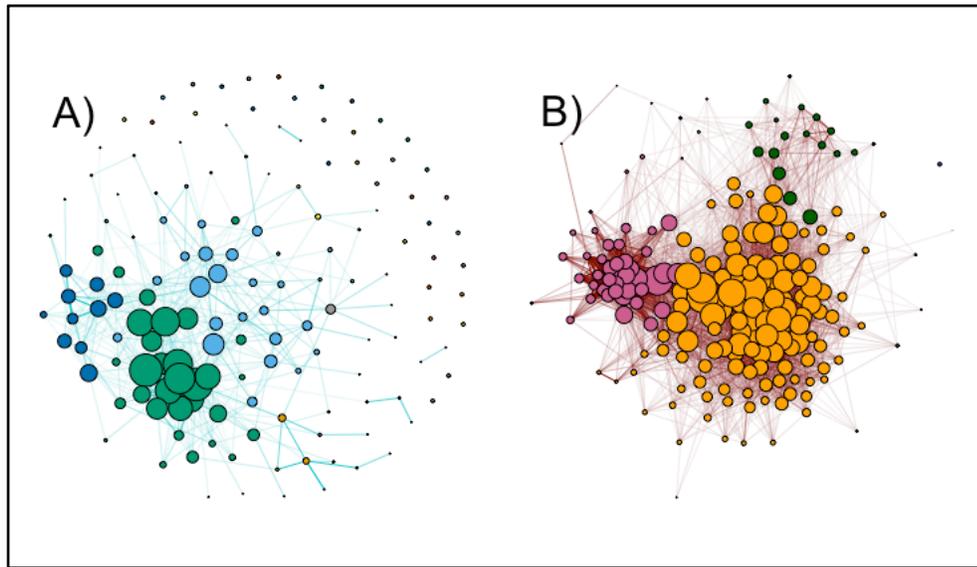


Figure 4 Social Networks of A) Atlantic sturgeons and B) sand tigers in 2012. Nodes are colored by walktrap community placement. The size of each node (AS = 146: ST = 201) represents the proportion of time that individual was detected within that network. Dyad (AS = 946: ST = 9,618) width represents association strength.

The double permuted null models did not provide significant evidence of assortment in Atlantic sturgeon by maturity, sex, or natal spawning river. Sand tigers did not display significant sex-based dis(assortment) although there was evidence for maturity-based assortment for sand tigers in the Delaware Bay ( $A = 0.143$ ,  $P < 0.003$ ) (Table 3). Slight significant assortment was also observed in the multispecies network ( $A = 0.034$ ,  $P < 0.032$ ; Figure 5). This suggests a stronger attraction between conspecifics than between mixed species (Farine et al., 2012).

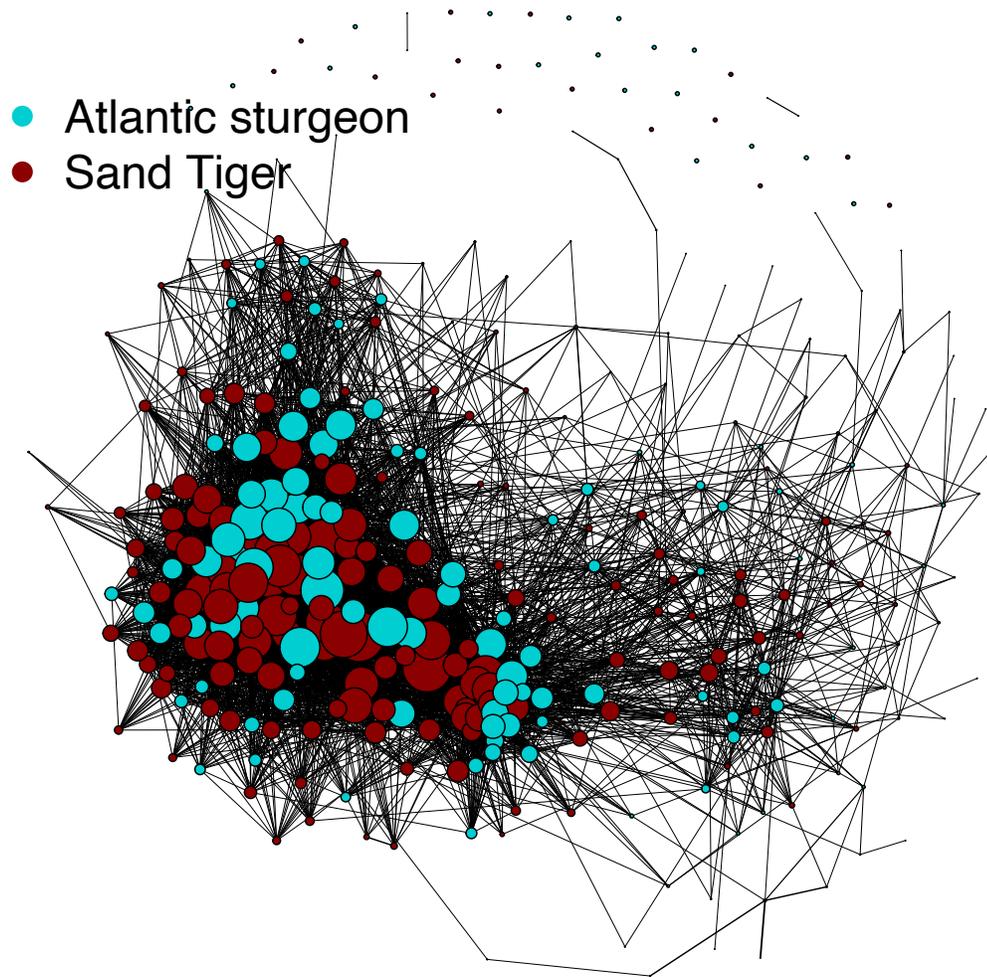


Figure 5 Social Network of Atlantic sturgeons and sand tigers in 2012. Nodes are colored by species. The size of each node represents the proportion of time that individual was detected within that network. Dyad ( $n = 11,268$ ) width represents association strength.

## Chapter 4

### DISUSSION

Over the past two decades, social networks have exposed many of the underlying social structures in marine environments. The accuracy of these networks is dependent upon the careful consideration of data collection and network design. The spectral analyses revealed evidence for environmental mediation on hourly network structures. I constructed social networks that accounted for environmental periodicity and provide evidence for complex social structures of sand tigers within the Delaware Bay. In addition, despite further evidence of aggregations at the mouth of the Delaware bay, there was no evidence to suggest an underlying social structure of Atlantic sturgeon.

Ideally, networks should be produced over time spans larger than the frequency of interference caused by environmental conditions. This is because fluctuations in environmental conditions are known to influence the detection range of acoustic receivers (Kessel et al., 2014), and thus may potentially bias the generation of social networks and their associated metrics. The 6.2 and 12.4-hour frequencies are consistent with the Delaware Bay's near semidiurnal tidal regime and diurnal patterns in sea breeze (NOAA, 2021; Simpson, 1994; Sonu et al., 1973). Temperature and pressure differences between the surface of the land and sea produce a daytime sea breeze and nocturnal land breeze (Simpson, 1994; Sonu et al., 1973). The increased wind speeds create shear stress on the water's surface, producing a wind stress signal of 12.4 hours (Sonu et al., 1973). Similar to this frequency is a strong signal in tidal height at 12.4 hours. As a result of the Delaware Bay's near semi-diurnal tidal regime, the region experiences almost two complete high and two low tides daily (Sharp, 2010

The semidiurnal tide also produces a 6.2-hour signal in the change in tidal height from four tidal currents each day (Sharp, 2010). Our spectral analyses revealed that the periodicity of environmental variables frequently overlapped with those of the network metrics and detections. This suggests that detections and network composition were influenced by the dynamic environment of the Delaware Bay. Thus, the influence of the environment on acoustic conditions also impacts the metrics of short-term (hourly) social networks. These results are consistent with previous research that found the variations in detection range amongst receiver types to influence association strengths and an individual's position within a network (Mourier et al., 2017). Therefore, caution is needed when constructing aquatic social networks from acoustic telemetry observations and these dynamics should be accounted for. Further, difficulties in comparing network metrics may be complicated by differences in environmental conditions between locations where communities are located.

Our nine-day sampling periods produced social networks over periods greater than the dominant environmental period affecting acoustic conditions in the Delaware Bay. Atlantic sturgeon SNA displayed no evidence for sociality using metrics of preferential co-occurrence (preferential and avoided associations), modularity or assortment. Conversely, sand tiger SNA showed significant preferential co-occurrence (preferential and avoided associations) and significant maturity-assortment (bias in associations formed between individuals of the same maturity state). As immature and mature sand tigers had overlapping patterns of distribution within the study site (See Figure 6), the maturity-assortment bias is likely a social structure inherent to the population. While it is difficult to speculate on the drivers of sociality, maturity assortment may be the result of intra-species aggression, as immature sand tigers avoid

the presence of more aggressive and dominant individuals. Using the 0.5 Q threshold, neither species exhibited robust community structures. However, sand tigers exhibited a significant modularity metric. The walktrap algorithm identified three primary community clusters (Orange, Pink, and Green) (See Figure 4). The green community occurred most often in the lower eastern side of Delaware Bay. The orange and pink communities overlapped on the western side of Delaware Bay, and in the Delaware coastal ocean (See Figure 7). Therefore, it is possible that these groups of sharks show some degree of preferential habitat use that could be driving a significant, but weak modularity statistic. These three groups do not appear to be aggregating by size or sex; therefore, future studies should focus on characterizing the habitat differences on the western and eastern side of the lower Delaware Bay to understand how habitat potentially structures their aggregations.

Atlantic sturgeon (Dunton et al., 2015; Laney et al., 2007; Taylor et al., 2016) and sand tigers (Gilmore et al., 1983) are known to form conspecific aggregations. The majority of the Atlantic sturgeon detections during our study period (63%, n = 62,886) occurred between four high activity receivers located at the mouth of the Delaware Bay (See Figure 8). Further, a substantial portion of all Atlantic sturgeon detections (39%, n = 38,109) occurred at a single receiver. This aggregation behavior is likely a driver of the bias in association by conspecifics seen in the mixed-species network. Similarly, despite lacking significant network metrics, the sturgeons' disproportionate use of four receivers may reflect the aggregating behavior previously documented in this species at the mouths of bays (Dunton et al., 2010; Laney et al., 2007). Rather than being social aggregations, these aggregating behaviors may be driven by environmental or foraging opportunities (Breece et al., 2018 a; McLean et

al., 2013 b). A crucial task of managers is the protection of habitats deemed critical for the recovery of an endangered species (Fisheries, 2021). As the Delaware Bay's Atlantic sturgeon aggregations are likely driven by environmental parameters, population recovery may be dependent on the protection of these key locations. However, our results differ from those reported for Atlantic sturgeon from the Minas Basin, Canada, which documented significant *CV* in one out of three study years (Lilly et al., 2020). Differences in observed sociality could arise from several sources, including behavioral differences amongst populations, acoustic array size and spacing, and habitat use.

While it is difficult to speculate on the definitive motivations for aggregations in marine species, the presence of significant *CV* and maturity-assortment metrics may indicate sociality as a driver or by-product of sand tiger aggregations in the Delaware Bay. The maturity assortment of sand tigers is consistent with the behaviors of migrating individuals, which have been observed forming size-discriminating groups (Haulsee et al., 2016 ; Kneebone et al., 2014; Teter et al., 2015). However, sex-assortment was not observed in the sand tiger network, a behavior known to exist amongst migratory groups (Haulsee et al., 2016; Teter et al., 2015) and elasmobranchs in particular (Mucientes et al. 2009). Haulsee et al., (2016), found that amongst sand tigers, social structures were not fixed. While in the bay it appears that sand tigers may provisionally disband from their sex-based association behaviors (Haulsee et al., 2016) although the drivers of this behavior are not understood. Further research is needed to investigate how the sociality of sand tigers' changes over time in the Delaware Bay.

Complex sociality and cognitive abilities have been hypothesized to coincide with the high brain-to-body mass ratios found within primates and other mammals

(Kamil et al., 2004; Street et al., 2017). While most fish possess brains that are comparatively small amongst vertebrates; typically, 1/15th the mass of a similarly sized bird or mammal (Helfman et al., 2009), some elasmobranchs possess brain-to-body mass ratios comparable to mammals (Northcutt, 1977; Yopak et al., 2007) suggesting the cognitive capacity for complex social behavior. As studies have begun to elucidate the social structures found within sharks (Anderson et al., 2021; Armansin, 2016; Haulsee et al., 2016; Jacoby et al., 2010 & 2016; Mourier et al., 2012; 2017; Papastamatiou, 2020), large brain-to-body ratio is hypothesized to be a driving factor of their complex social structures (Haulsee et al., 2016; Jacoby et al., 2010). To our knowledge, the brain-to-body weight ratio of Atlantic sturgeon has not been documented. However, the closely related white sturgeon (*A. transmontanus*) has a brain-to-body weight ratio (0.19 brains mg/body g) near five times smaller than that of sand tigers (0.89) (Albert et al., 1999; Crile & Quiring, 1940; Yopak et al., 2007). Therefore, the relative contrast in brain-to-body weight could be argued as a driver for the differences in sociality seen between these species. Sand tigers possess large brain-to-body mass ratios when compared to sturgeon and other fishes. (Albert et al., 1999; Crile & Quiring, 1940; Froese & Pauly, 2010; Yopak et al., 2007). However, amongst elasmobranchs, their ratio is small (Northcutt, 1977; Yopak et al., 2007). Assuming this ratio is a predictor of potential social complexity, it is likely that other species of elasmobranch with greater brain-to-body mass ratios form social structures of even greater complexity.

A common assumption among animal social networks is the gambit-of-the-group condition. The gambit-of-the-group assumes all individuals within close spatiotemporal proximity are in association (Franks et al., 2010; Whitehead & Default,

1999). Thus, this method may overestimate the association between individuals utilizing the same habitat. As this and prior research (Mourier et al., 2017) have demonstrated, transmitter detection range likely plays a role in network analyses. The incorporation of a nine-day sampling period mitigated the influence of the environment on metrics by calculating association strength over periods greater than the primary environmental variables that impact the detection range of acoustic receivers in Delaware Bay. Nevertheless, the large detection ranges of VEMCO equipment (efficiency < 10% at 600m) may influence the generation of the network metrics as individuals detected to co-occur may in reality be separated by hundreds of meters (Mourier et al., 2017). Comparing network metrics between communities and species remains a basic challenge, as metrics are influenced by the network's composition (Farine and Whitehead, 2015). At no point in these analyses were observed metric values directly compared across networks. Rather, the value of each observed social network metric (CV, Q, and assortment) was compared to the distribution of their respective permutations (Bond et al., 2021).

In summary, spectral analysis revealed the impact that environmental conditions have on social network metrics, likely through influencing the acoustic receiver detection range. Researchers should exercise caution when producing networks of small temporal scales and when comparing networks between locations. SNAs should be produced over time spans greater than the periodicity of the predominant environmental variables within their study site, or the impact of changing environmental variables on acoustic conditions should be characterized. Additionally, results from the social networks suggest Atlantic sturgeon display little evidence of complex social structure in the Delaware Bay. In contrast, sand tigers' networks

exhibited evidence for maturity assortment and preferential co-occurrence. Finally, a mixed-species network suggests preferential assortment by conspecifics.

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## Appendix

### SUPPLEMENTARY MATERIALS

Table 4 Linear regressions estimated (Est.) the impact of environmental variables (retriever from NOAA's Brandywine Shoal Light (Station ID: 8555889) on detection frequency of Atlantic sturgeon and (AS) sand tigers (ST) (June 9th - October 7th, 2012). Significant negative correlations were found between hourly measurements of change in tidal height (CTH) and wind stress (WS) and the number of detections per receiver. CTH was measured as the first derivative of hourly tidal height measurements (m) and wind stress as the wind speed squared (m/s)<sup>2</sup>. The goodness-of-fit for these models is indicated by adjusted R<sup>2</sup>.

	CTH Est.	CTH	WS Est.	WS	R2
AS	-0.368	P = 1.44e-16	-.002	P < 2e-16	0.033
ST	-0.197	P < 5.12e-14	-.001	P = 5.12e-14	0.024

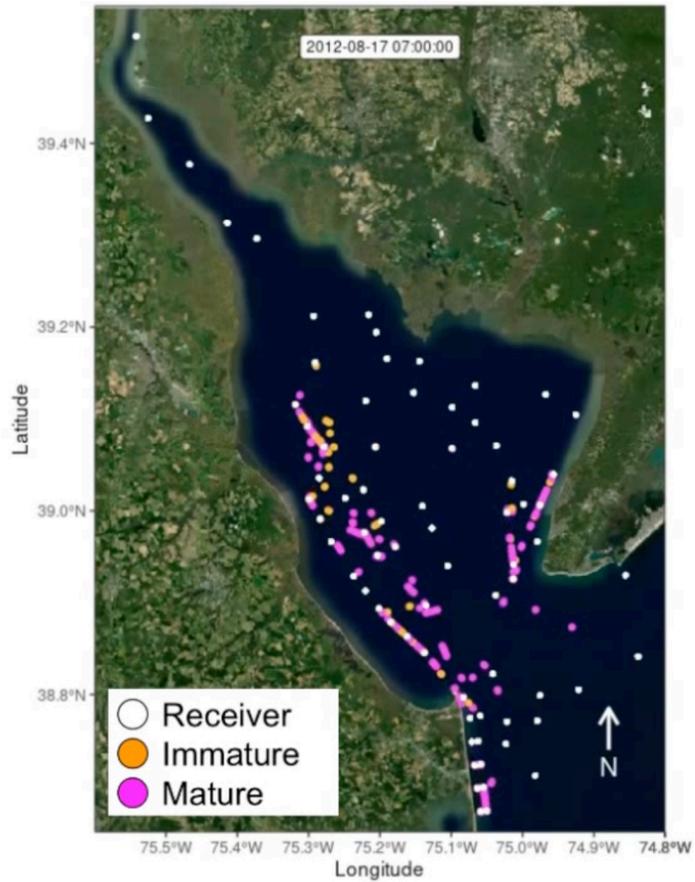


Figure 6 Video of sand tiger movement in the study site from 2012-05-14 to 2012-10-14. Individuals are colored by their maturity state. Video generated with the R package moveVis (Schwalb-Willmann et al. 2020). To watch the video online, please visit <https://www.youtube.com/watch?v=FuU-TqRozS4>

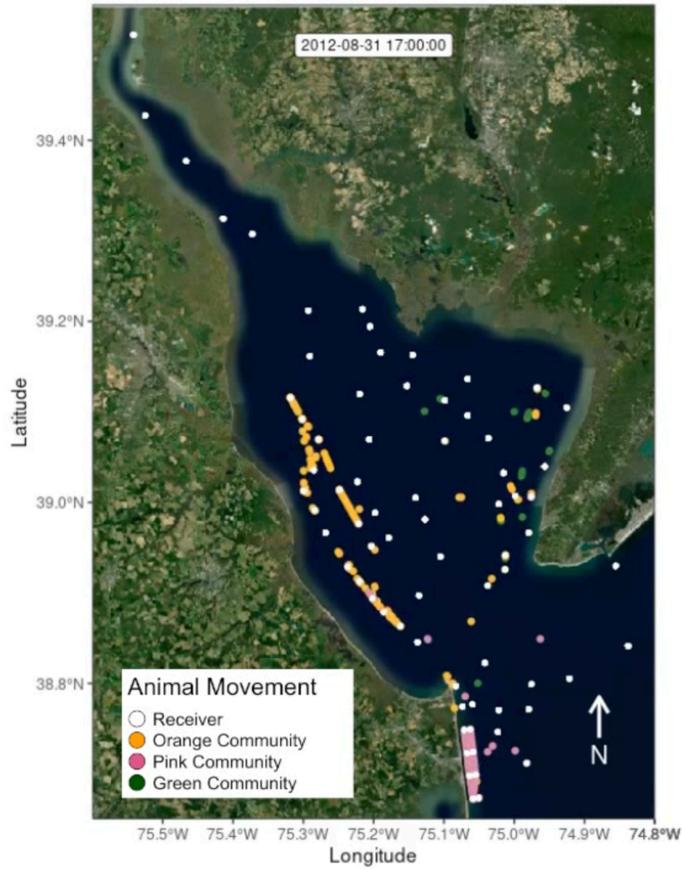


Figure 7 Figure.6) Video of sand tiger movement in the study site from 2012-04-19 to 2012-10-15. Individuals are colored by their community as identified by the walktrap algorithm. Video generated with the R package moveVis (Schwalb-Willmann et al. 2020).  
<https://www.youtube.com/watch?v=lv2JuaT0mM>

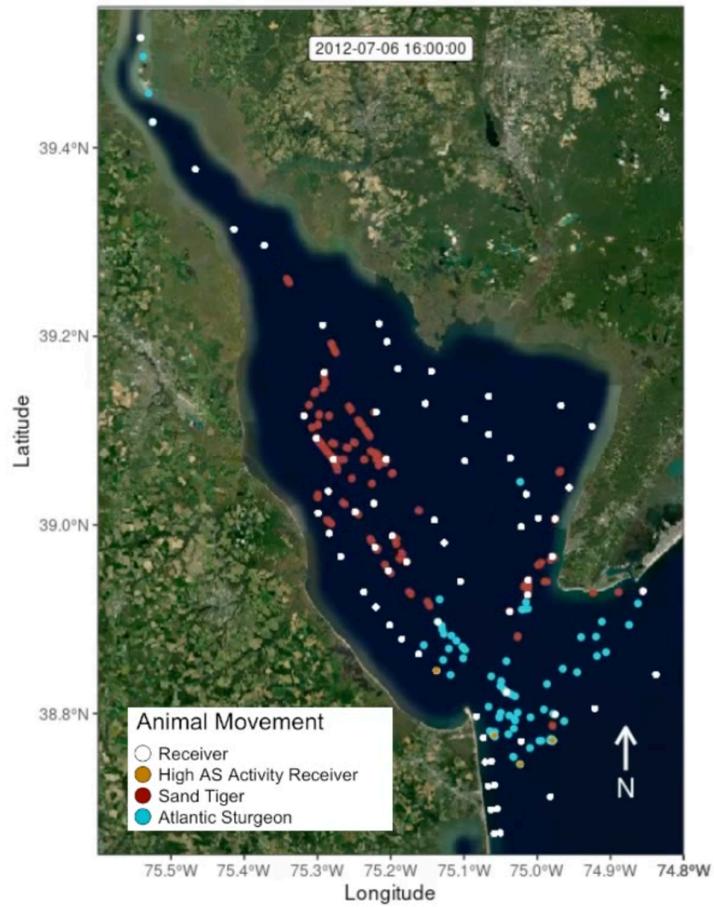


Figure 8 Video of Atlantic sturgeon (AS) and sand tiger movement in the study site from 2012-03-21 to 2012-11-23. Video generated with the R package moveVis (Schwalb-Willmann et al. 2020). To watch the video online, please visit <https://www.youtube.com/watch?v=i7c8j1T-TJo>