FEEDING ECOLOGY AND MOVEMENT PATTERNS OF

ATLANTIC STURGEON IN MINAS BASIN, BAY OF FUNDY

by

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Atlantic sturgeon are a highly migratory, anadromous species known to seasonally aggregate. The Minas Basin, Bay of Fundy, is a summer terminus for a large mixed-stock feeding aggregation consisting of primarily sub-adult and adult Atlantic sturgeon from Canada and the USA. The movement and feeding behaviour of Atlantic sturgeon was examined in a macro-tidal estuary, and an attempt to link these behaviours to their physical and biotic drivers was made. Diet analysis revealed that tube-dwelling polychaetes comprised the majority of the Atlantic sturgeon diet. Quantification of movement patterns and analysis of fine-scale spatial data revealed three distinct behaviours exhibited by acoustically tagged Atlantic sturgeon. The first movement pattern was indicative of foraging, and the second of searching over the intertidal mudflats, whereas the third movement type suggested transitory behaviour moving past the general study site. Increased crepuscular activity was also identified revealing a diel pattern of behaviour not previously described for Atlantic sturgeon in the marine environment. Quantitative identification of foraging behaviour and diet analysis indicate that the Kingsport Beach area in the Southern Bight of the Minas Basin is an important feeding site for Atlantic sturgeon. More information on the basic biology of the Atlantic sturgeon is required in order to develop a holistic approach to the management and conservation of this trans-boundary species, particularly at mixing sites such as Minas Basin.

LIST OF ABBREVIATIONS AND SYMBOLS USED

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ANOVA: Analysis of variance

°C: degrees Centigrade

FL: fork length

g: grams

Ir: Hureau's index of gut fullness

IRI: Index of relative importance

km: kilometer

L: litre

m/s: meter per second

m: meter

mg/L: milligram per litre

MS222: 3-amino benzoic acid-ethyl-ester-methane-sulfate

%N: percent abundance

%O: percent occurrence

ROM: rate of movement in m/s

SD: standard deviation

um: micrometer

VPS: Vemco Positioning System

%W: percent weight

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GENERAL INTRODUCTION

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The Atlantic sturgeon, *Acipenser oxyrinchus* Mitchill, 1815, is an anadromous and

highly migratory species that has been recognized as an economically important

commercial fish and has been sought by North American natives since they first occupied

North America (Saffron 2004) and by European settlers since the 1600s (Scott and Scott

1988). Before a Russian settler discovered how to properly preserve and ship caviar to

Europe in the late 1700s, sturgeon was only consumed by the natives or sold to

southerners to feed to slaves (Saffron 2004). In the 1800s carcasses were boiled down to

produce high quality oil and eventually the meat was widely distributed and consumed

fresh, pickled or smoked; while caviar was made by curing the eggs with salt and was

considered a delicacy (Vladykov and Greeley 1963; Smith 1985; Saffron 2004). Other

important uses were found for the swimbladders, as they were dried and made into

isinglass, which was then used to clarify wine and beer or as an adhesive (Smith 1985;

Dadswell 2006).

The fisheries for sturgeon have greatly declined in the last 100 years, due to over-

harvesting pressures as well as pollution and blockage of spawning rivers by dams (Hoff

1980; Dadswell 2006). Towards the end of the 19th century, catches for certain years

could reach over 2267.9 metric tonnes (mt) for all species of sturgeon combined.

However by 1956, catch rates had dropped to only 177.8 mt in Canada and 326.1 mt in

the United States of America (U.S.) (Hoff 1980). In 1979, Atlantic sturgeon received an

Appendix II listing by the Convention for the International Trade of Endangered Species

(CITES), which limits the trade of any part of this species between participating

countries. To relieve fishing pressures in the U.S., a moratorium on Atlantic sturgeon fishing was set in the exclusive economic zone of participating states (ASMFC 1990) and by 1998 all American fisheries were closed for the species. In 2010, a joint decision was made by National Oceanic and Atmospheric Administration (NOAA) Fisheries Service and the U.S. Fish and Wildlife Service to not list Atlantic sturgeon under the Endangered Species Act (NOAA 2010). In 2012, however, that decision was revised and four of the five distinct population segments (DPSs) in the United States were listed as endangered including the New York Bight, Chesapeake Bay, Carolina, and South Atlantic (NOAA 2012 a,b). The Gulf of Maine DPS was listed as "threatened" under the same listing (NOAA 2012 a,b). A single DPS consists of a number of spawning rivers close enough in proximity and in the same ecotone to allow genetic mixing (i.e. individual spawners could potentially spawn in any of the spawning rivers within that DPS). Currently there are 20 known spawning rivers for Atlantic sturgeon in the U.S. (NOAA 2012 a,b).

In Canada, the Saint John River, New Brunswick and the St. Lawrence River, Quebec are home to the two known spawning stocks of Atlantic sturgeon, both of which currently support directed fisheries (Dadswell 2006; DFO 2009 a). Recently in the Maritime Provinces of Canada, populations were listed as threatened by the Committee on the Status of Endangered Wildlife in Canada (COSEWIC) under the Species At Risk Act (SARA). This listing was based on the assumption that the entire population is solely sustained by the spawning stock located within the Saint John River (COSEWIC 2011) but neglected to include a known historical population that may persist in the Annapolis River, Nova Scotia (Dadswell 2006).

Atlantic sturgeon are distributed along the eastern coast of North America from northern Labrador to southern Florida (Dadswell 2006). In Canada, spawning is in June and July, however more southern populations spawn in mid to late February (Vladykov and Greeley 1963), the spring (Van Eenennaam et al. 1996) and/or the fall (Collins et al. 2000). The Gulf sturgeon (*Acipenser oxyrinchus desotoi*), a southern subspecies to Atlantic sturgeon, have been documented to spawn in the spring (Sulak and Clugston 1998; Sulak and Clugston 1999). Adult Atlantic sturgeon generally migrate into freshwater in advance of the spawning season, with males arriving prior to females (Bigelow and Schroeder 1953). Water temperature is thought to be the cue for ripe adults, which will then migrate back to sea once spent (Smith 1985). Non-annual spawning appears to be normal for Atlantic sturgeon. Most males have been shown to spawn every 1-2 years (Van Eenennaam et al. 1996; Collin et al. 2000; Dadswell 2006), however one study recognized a maximum of 4.5 years in between spawning events (Smith et al., 1982). Females appear to have longer spawning intervals, with estimates ranging from 2-3 years (Vladykov and Greeley 1963) to 5+ years (Smith et al. 1982; Dadswell 2006).

Adhesive eggs are widely dispersed by the female over the coarse sediment of a freshwater river bed, where they will eventually settle and hatch within one to two days. Yolk-sac larvae are cryptic post-hatch and remain in interstitial spaces until the yolk sac is absorbed (Kynard are Horgan 2002). At approximately 16 mm in length, larvae swim up into the water column and drift downstream to freshwater or estuarine habitats with soft sediments (Kynard and Horgan 2002). Juveniles will then spend 1-12 years in the mesohaline portion of estuaries before continuing their migration to sea (Dadswell 2006). While in the marine environment, Atlantic sturgeon will spend 5 to 15 years before they

are ready to migrate back to spawning grounds once they have reached sexual maturity (Dadswell 2006).

Maturation age and size are dependent on sex as well as location of the natal stream (Vladykov and Greeley 1963; Dadswell 2006). On average, southern populations mature more quickly. Female Gulf sturgeon in the Suwannee River, FL, are sexually mature at 8-12 years of age and males at 7-10 years (Huff 1975). In South Carolina, females will spawn at 7-19 years and males at 5-13 years (Smith 1985). Moving further north, in the Hudson river, NY, females do not reach maturity until 20-30 years and males 11-20 years (Dovel 1979). These maturation ages are somewhat similar to those of individuals found in the St. Lawrence River, Canada, where females mature between 27-28 years (Scott and Crossman 1973) and males between 16-34 years (Scott and Crossman 1973; Caron et al 2002).

Generally during periods of marine residency Atlantic sturgeon aggregations will form on foraging grounds such as in Minas Basin (Wehrell 2005; Dadswell 2006; Wehrell et al., 2008). Because of the species highly migratory nature, a great degree of stock mixing occurs at these aggregation sites (Dadswell 2006; Wirgin et al. 2012). Microsatellite DNA and mitochondrial DNA control region sequence analysis of the Minas Basin summer aggregation of Atlantic sturgeon was used to determine that it is >60% comprised of individuals natal to the St. John River, NB, with a 34-36% contribution from the Kennebec River, Maine, about a 1-2% contribution from the Hudson River, New York, and <1% from the James River, Virginia (Wirgin et al. 2012). Little is known about the summer feeding aggregation of Atlantic sturgeon in Minas Basin, however, recent population estimates suggest that approximately 9 000 to 10 000

sub-adult and adult sturgeon occupy the area from April - November (Wehrell and Dadswell *unpublished data*).

Feeding ecology

Atlantic sturgeon are primarily benthic feeders which use their inferior placed protrusible mouth to ingest large sections of sediment with a high suction force. Because much of their time is spent in water with low visibility, feeding is done by using a combination of olfactory and taste chemosensory cues and electroreceptors (Miller 2004). Many food habit studies infer an opportunistic feeding behaviour, which suggests that these fish will prey on whatever suitable types of food items are available in a particular area (Vladykov and Greeley 1963; Mason and Clugston 1993; Johnson et al. 1997; Brosse et al. 2000; Miller 2004; Nilo et al. 2006).

Diet studies on sturgeon are relatively limited, primarily due to the difficulties associated with retrieving stomach contents from live fish (Haley 1998). Previous studies examined the entire alimentary canal of sacrificed fish in order to assess and quantify diet and feeding habits (Valdykov and Greeley 1963; Mason and Clugston 1993). The sacrifice of many individuals is no longer possible now that many *Acipenser* spp. populations are threatened or endangered. Different techniques for retrieval of stomach contents from live fish have been explored on a number of species including many sturgeon spp. (e.g., large-mouth bass *Micropterus salmonides* and grass pickerel *Esox americanus vermiculatus*, Foster 1977; Atlantic sturgeon, Johnson 1997; Haley 1998; Savoy 2007; juvenile European sturgeon *Acipenser sturio*, Brosse et al. 2000; farmed Siberian sturgeon *Acipenser baerii*, Brosse et al. 2002; juvenile lake sturgeon *Acipenser*

fulvescens, Nilo et al. 2006). The predominant method used has been gastric lavage, which employs pulsated water through a tube into the fish's stomach causing food particles to release from the digestive tract and move out through the oesophagus and mouth. The success of this method of food retrieval has been well documented and it is now a recommended procedure by NOAA for use on Atlantic sturgeon (NOAA 2010).

An early attempt at gastric lavage on an individual Gulf sturgeon was a failure, as the sturgeon would not regurgitate anything (Mason and Clugston 1993). Since the completion of this food habit study in the Suwannee River, Florida, a number of others have reported successful use of this procedure. Many studies appear to use a modified version of Brosse et al. (2002), which involved pulsated water with a pressurized tank. This procedure had previously been modeled after Nilo's (1996) study on lake sturgeon, and was improved for increased efficiency; both in terms of percent food retrieval as well as decreased time of use (Brosse et al. 2002). When used on force fed farmed Siberian sturgeon, the improvised technique recovered items from 100% of tested fish, thus leading to the conclusion that using a pressurized water reservoir enables rapid gastric lavage compared to other methods (Brosse et al. 2002), such as the syringe method used by Haley (1998). This in turn allows for limited handling time of captured fish, which could be associated with stress level (Brosse et al. 2002) and could also lead to faster release of wild fish close to their capture site. High recovery rates were also reported in both lake sturgeon and Atlantic sturgeon, as food items were recovered from 96% (Nilo 1996) and 91% (Haley 1998) of the individuals sampled, respectively.

Following the lavage procedure by Brosse et al. (2002) all sturgeon were sacrificed to examine the stomachs. The type of prey significantly influenced the

recovery with larger shrimp and fish having a higher recovery rate than smaller earthworms and chironomids, which may have led to a distorted picture of the actual diet of sturgeons examined. Similarly Foster (1977), Nilo (1996), and Haley (1998) suggest that these biases need to be considered in any study employing a food retrieval method where stomachs cannot be examined post-procedure.

Food studies can give us a better understanding of a species major foraging areas, which could direct protection of essential habitat (Johnson et al. 1997; Brosse et al. 2002). Identifying preferred prey types could also lead to possible improvements in captive feeding and rearing (Brosse et al. 2000). The first step in examining food habits is to identify ingested prey species in all areas of an individual's habitat (Johnson et al. 1997). For Atlantic sturgeon, their habitat includes freshwater river systems, estuaries, coastal and offshore marine habitats. It has been suggested that sturgeon species feed opportunistically on what is available to them in their immediate surroundings (Brosse et al. 2000; Nilo et al. 2006). This would theoretically suggest a shift in diet composition depending on location and available prey, as well as a diverse diet in areas with high prey diversity.

Studies on Atlantic sturgeon suggest a diet consisting primarily of soft bodied invertebrates and occasionally small fish, such as the American sand lance (*Ammodytes* spp., Vladykov and Greeley 1963; Dadswell 2006). In the freshwater portion of the St. Lawrence River, 31 taxa were identified in Atlantic sturgeon stomachs, with gammarids and oligochaetes representing the most important prey items, both by percent occurrence and weight (Guilbard et al. 2007). These results were found to vary based on age. Age 0 and juveniles had a less diverse diet regime with gammarids as the primary prey, whereas

the adult diet consisted more of oligochaetes. Similarly, season had an effect on diet composition, with gammarids and chironomids being more prominent in fall and oligochaetes in summer. Occasionally nematodes, aquatic insects, and larval Atlantic tomcod (*Microgadus tomcod*) were identified in some of the sampled individuals (Guilbard et al. 2007). These results support those observed by Vladykov (1948), who was the first to publish stomach content results for Atlantic sturgeon in the St. Lawrence River. He only reported 14 taxa, however, the trends were the same with predominant prey consisting of oligochaetes and gammarids. Similarly, Vladykov (1948) recognized an ontogenous shift in feeding behaviour, with gammarids being more prominent in young (age 0) individuals.

Several studies have identified polychaetes as the primary prey for Atlantic sturgeon in estuaries and in coastal and offshore marine habitats. In the Hudson River estuary, juvenile and sub-adult diets consisted of polychaetes and to a lesser extent, isopods and amphipods (Haley 1999). In the Connecticut River estuary (Savoy 2007), lower Cape Fear River in North Carolina (Moser and Ross 1995) and off the Central New Jersey coast (Johnson et al. 1997), sub-adults and adults fed mostly on polychaetes and various other invertebrates in small numbers. It is also common to find vegetal matter in examined stomachs, as most Atlantic sturgeon ingest organic and inorganic detritus incidentally during feeding (Mason and Clugston 1993). Although many studies do not quantify the inorganic material, it has been suggested that digestible biofilm and substances extracted from the vegetal matter could constitute an additional nutritional source for the consumer (Mason and Clugston 1993).

Diet analyses of other sturgeon species reveal a large portion of prey consumed are soft-bodied organisms (Table 1.1). This is particularly the case with lake sturgeon which cohabit the freshwater portion of the St. Lawrence River estuary with Atlantic sturgeon. A comparison of diet between the sympatric species led to the discovery that much of the same prey is consumed, such as gammarids and oligochaetes (Guilbard et al. 2007). However, the diet of the lake sturgeon was more diverse than that of the Atlantic sturgeon, and included a higher number of mollusks, such as sphaeriid bivalves and gastropods, and even zebra mussels (Guilbard et al. 2007). Other sturgeons appear to consume a higher proportion of prey with harder exoskeletons and even fish. The Gulf sturgeon, for example, consumes mainly arthropods and annelids, however mollusks have also been found in their diet (Mason and Clugston 1993). The white sturgeon (*Acipenser transmontanus*, McCabe et al. 1993) and the Russian sturgeon (*Acipenser gueldenstaedttii*; Zolotarev et al. 1996) have diets consisting of primarily mollusks, and the shortnose sturgeon (*Acipenser brevirostrum*) feeds heavily on mollusks, changing from clams in more saline portions of estuaries to gastropods in freshwater marshes (Dadswell 1979; Dadswell et al. 1984 a). The most diverse diet, however, is that of the beluga sturgeon (*Huso huso*), an inhabitant of the Sea of Azov. It has been noted to consume a variety of larger prey, including shad (*Alosa*), anchovy (*Engraulis*), aquatic birds and even baby seals (Pirogovskii et al. 1989).

Table 1.1. Summary of diet composition for many North American sturgeon species. FW = freshwater; Est = estuarine; Mar = marine.

Species	Habitat	Life Stage	Primary Prey	Secondary Prey	Citation
A. oxyrinchus	FW	Age-0/juvenile	Gammarids	Oligochaetes	Vladykov 1948
	FW	Adult	Oligochaetes	Gammarids	Guilbard et al. 2007
	Mar	Sub-adult/adult	Polychaetes	Amphipods/isopods	Johnson et al. 1997
	Est	Juvenile/sub-Adult	Polychaetes		Haley 1999
	Est	Sub-adult/adult	Polychaetes		Moser and Ross 1995; Savoy 2007
A. o. desotoi	FW	Age-0	Insects/ oligochaetes		Mason and Clugston 1993
	FW	Juvenile	Amphipods/ isopods		Mason and Clugston 1993
	Est	Sub-adult/adult	Crustaceans	Polychaetes/gastropods	Mason and Clugston 1993
A. fulvescens	FW	Age-0	Baetiscids/ chironomids	Nematodes	Guilbard et al. 2007 Guilbard et al. 2007
	FW	Juvenile	Gammarids	Tomcod YOY	Guilbard et al. 2007
	FW	Sub-adult	Crustaceans	Amphipods/annelids	Nilo 1996
A. brevirostrum	FW	Juvenile	Crustaceans	Insect larvae	Dadswell 1979; Dadswell et al. 1984 a
	FW	Adult	Mollusks		
A. transmontanus	FW	Juvenile	Crustaceans	Mollusks	McCabe et al. 1993

Minas Basin intertidal ecology

The inner Bay of Fundy is a warm summer enclave and supports the foraging of numerous migratory aquatic organisms (Dadswell et al. 1984 b; Dadswell 2006). Off the coast of New Brunswick, Atlantic sturgeon feeding pits have been observed in great abundance on the intertidal mudflats and represent an important erosional-depositional force within that area of localized feeding (Pearson et al. 2007). Similar foraging occurs on the Minas Basin mudflats, but there is currently no published research on Atlantic sturgeon feeding behaviour and ecology for that area. Literature regarding a number of intertidal benthic foragers, however, is available for Minas Basin. A common feature in all intertidal foraging literature for Minas Basin is the amphipod *Corophium* spp., as a key prey item. *Corophium* exist in densities as high as 60 000/m^2 and have been found to comprise much of the diet for migrating shore birds such as the Semipalmated sandpiper (*Calidris pusilla*; Gratto et al. 1984; Hicklin and Smith 1984), groundfish including the winter (*Psuedopleuronectes americanus)* and smooth flounders (*Liopsetta putnami;* Dadswell et al. 1984 b; McCurdy et al. 2005), Atlantic tomcod (*Macrogadus tomcod*; Salinas 1981; Dadswell et al. 1984 b) and winter skate (*Leucoraja ocellata*; McCurdy et al. 2005), as well as some pelagic fishes such as the Atlantic silversides (*Menidia menidia*; Gilmurray and Daborn 1981; Imrie and Daborn 1981), American smelt (*Osmerus mordax*; Imrie and Daborn 1981), and mummichog (*Fundulus heteroclitus*; Dadswell et al. 1984 b). For many of these species, particularly benthics, foraging is favourable in the intertidal mudflats because of the patches of high density prey buried in the soft and easily accessible sediment. Much of the Minas Basin intertidal is comprised

of soft silty-sand and mud making it rich in tube-dwelling polycheates, amphipods, and crustaceans (Bousfield and Leim 1959; Hicklin and Smith 1984).

Movement in the intertidal

Foraging and feeding behaviour is likely to differ in the Minas Basin from the behaviour of foraging fishes in other ecosystems. Foraging and feeding are likely influenced by tidal variations and limited temporal access to the intertidal mudflats. When flounder were ultrasonically tracked in an estuary affected by tides, they were found to forage according to tidal state (Wirjoatmodjo and Pitcher 1984). At high tide flounder movements were characteristic of active foraging. As the tide began to fall, flounders increased their swim speed in what was described as an effort to complete feeding while invertebrates were still available, and to avoid stranding.

The use of tracking technology in order to better understand movements and to identify various animal behaviours is not novel and has been used on aquatic fishes and mammals alike. Due to rapid advances in technology multiple individuals from a population can be tracked simultaneously in order to answer questions about the population through the individual (Heupel and Heuter 2001; Heupel et al. 2004). Acoustic tags use the transmission of sound signals at frequencies, generally around 69 kHz (69, 000 cycles/sec) and send out pulses of information including an individual ID code, time and date stamp, and occasionally physical data such as temperature and/or pressure (i.e. depth; Stokesbury et al. 2009). Due to water's absorptive properties, underwater transmission of data is difficult, therefore ultrasonic frequencies are favoured over radio frequencies because they are less readily absorbed. Acoustic transmissions are

detected by active or passive receiving devices that either store the information or relay it in real time. Passive tracking is more efficient when studying enigmatic aquatic animals, particularly top predators, as it is usually difficult to actively follow them for extended periods of time (Simpfendorfer et al. 2002).

Telemetry in general has allowed researchers to determine species natural histories (Stokesbury et al. 2009) and answer questions important to management for fish captured in the recreational (*Micropterus* spp*.*, Cooke et al. 2000; *Albula* spp., Cooke and Philips 2004; *Morone saxatilis,* Gilroy et al. 2010), and commercial (Welch et al. 2002; Farrell et al. 2008) fishing sectors. Acoustic telemetry has also been used to test hypotheses important to the development of conservation strategies for near-threatened (Moser and Lindley 2007; Lindley et al. 2008), threatened (Fox et al., 2000) or endangered species (Hissmann et al. 2000; Welch et al. 2009). Information gained from threatened and endangered species often provides important and previously unknown discoveries about their life histories (Lindley et al. 2008). Often there are information gaps in our knowledge about species of concern that include life histories and the distribution and composition of critical habitat.

This technology has been readily used on Atlantic sturgeon to examine spawning periodicity (Collins et al. 2000; Caron et al. 2002), locate spawning grounds (Collins et al. 2000) and/or foraging sites (Kieffer and Kynard 1993), and to gain a deeper understanding of seasonal habitat use and general movements (Collins et al. 2000; Hatin et al. 2007; Simpson and Fox 2007; Fernandes et al. 2010). In addition, the use of pop-up satellite archival tags have given insight into Atlantic sturgeon coastal migrations (Erickson et al. 2011). However, there is a lack of studies on fine-scale movement

patterns and behaviours. Habitat use by telemetered animals in general has been described by spatial distribution through the use of kernel densities, convex polygons to estimate activity space (Heupel et al. 2004; Collins et al. 2007; Yeiser et al. 2008), and/or residency times (Holland et al. 1993; Collins et al. 2007). More recently, however, research has begun to shift towards the understanding of fine-scale behaviour due to its ability to tell us exactly how the animal is using the environment and what external factors (i.e. bathymetry, temperature, salinity, etc.) play a role in the animal's displacement within their habitat.

Simpfendorfer et al. (2002) used passive acoustic receivers in an array with overlapping detection ranges to calculate short-term centers of activity for tagged neonate blacktip sharks (*Carcharhinus limbatus*). This allowed for long-term movement and space utilization patterns to be investigated over broader areas. Center-of-activity calculations allowed for acoustic data to be used in a way that could answer in-depth ecological questions about the species, rather than providing simple presence or absence data (Simpfendorfer et al. 2002). Since then, Vemco has released a VR2W positioning system (VPS) which uses a weighted average of detections by telemetered animals within an array of receiving devices to obtain accurate positions of animals with small margins of error (mean positional accuracy of 2.64 ± 2.32 m; Espinoza et al. 2011 a), similar to calculating centers of activity but on a finer scale. The VPS has been used to assess fine-scale movement patterns on the gray smooth-hound shark (*Mustelus californicus*, Espinoza et al. 2011 b), shovelnose guitarfish (*Rhinobatos productus*, Espinoza et al. 2011 a; Farrugia et al. 2011), pouting (*Trisopterus luscus*, Reubens et al. 2011), Atlantic

cod (*Gadus morhua*, Dean et al. 2012), and lake trout (*Salvelinus namaycush*, Midell et al. 2012), but has not before been used to study Atlantic sturgeon behaviour.

Context for this research

Considerable knowledge gaps exist concerning the general biology of sturgeons. Highly migratory animals, such as the Atlantic sturgeon, have a complex life-history, inhabiting a variety of ecosystems. Researchers must be able to characterize the shift in the Atlantic sturgeon biology and habitat use as it moves throughout its range from freshwater rivers, to estuaries, and into the open ocean. The technical and scientific basis now exists to track the ocean movements of individual pelagic fish for extended periods of time, thus allowing the identification of migration pathways, important foraging and spawning grounds, and overall distribution and habitat use. This thesis is organized into two chapters. The first examines the feeding ecology of Atlantic sturgeon in the Minas Basin, while the second takes a quantitative approach at determining different movement patterns of acoustically tagged sturgeon as they utilize the intertidal mudflats. A general discussion follows these chapters to integrate the findings.

CHAPTER 1

FEEDING ECOLOGY OF ATLANTIC STURGEON ON

THE INFAUNA OF INTERTIDAL MUDFLATS

OF MINAS BASIN, BAY OF FUNDY

ABSTRACT

A large feeding aggregation of Atlantic sturgeon occupies the inner Bay of Fundy during summer, which mainly forages on the intertidal mudflats. Prey content of Atlantic sturgeon was examined during the summer of 2011 in Minas Basin. Atlantic sturgeon demonstrated an overall preference for sandy tube-dwelling polychaetes (Index of Relative Importance (IRI) = 99.7%). Major prey taxa included Maldanidae (*Clymanella* sp., 52.5%) and Spionidae, primarily species *Spiophanes bombyx* (41.6%). Other prey items consumed by Atlantic sturgeon diet included Phyllodocidae (*Eteone* sp., 2.1%), Nephtyidae (2.2%), Nereididae (0.7%), and Glyceridae including *Glycera dibranchiata* (0.6%). Seventeen additional taxa were identified in trace amounts (mean IRI = 0.02%), including Corophidae and Mysidae. There was no significant difference in the number of prey items consumed and fork length of the fish. Analysis of gut fullness with respect to tidal state indicated no significant difference between gut fullness on the flood or ebb tide. An overall preference for sandy tube-dwelling polychaetes may indicate that particular areas of the Minas Basin intertidal region are more important to these foraging fish than others. Considerable baitworm harvest occurs during summer months in Minas Basin and could potentially create impacts with sturgeon, both directly through competition for prey items and indirectly through change in sediment and benthic community composition.

INTRODUCTION

Atlantic sturgeon are an anadromous, and highly migratory species which once supported a large commercial fishery (Secor 2002). Atlantic sturgeon stocks along the east coast of North America collapsed in the late 1800's and again in the late 1900's due to overharvesting and habitat degradation. Sturgeon life history characteristics such as slow growth, late age of maturity, and periodicity of spawning make them vulnerable to overexploitation (Dovel and Berggren 1983; Smith 1985; Johnson et al. 1997; Dadswell 2006). A few spawning stocks of Atlantic sturgeon have been extirpated from historical spawning rivers (ASSRT 2007), but in some cases previously depleted populations have rebounded and are now stable and fished commercially (Trencia et al. 2002; Dadswell 2006; Kahnle et al. 2007).

There are two known spawning stocks of Atlantic sturgeon in Canada, one in the Saint John River, New Brunswick and one in the St. Lawrence River, Quebec. Each of these stocks currently supports directed fisheries (DFO 2009 a). Recently in the Maritime Provinces of Canada, populations were listed as threatened by the Committee on the Status of Endangered Wildlife in Canada (COSEWIC) under the Species At Risk Act. This listing was based on the assumption that the entire population is solely sustained by the spawning stock located within the Saint John River (COSEWIC 2011) but neglected to include a known historical population that may persist in the Annapolis River (Dadswell 2006). Also, four Distinct Population Segments (DPS) in the USA have been listed as endangered and one as threatened under the Endangered Species Act (NOAA 2012 a,b). The New York Bight, Chesapeake Bay, Carolina, and South Atlantic DPS' are

classified as endangered, whereas the Gulf of Maine DPS is classified as threatened (NOAA 2012 a,b).

From spring to fall each year an aggregation of approximately 9 000 to 10 000 sub-adult and adult Atlantic sturgeon migrate into the Minas Basin, Bay of Fundy (Wehrell 2005; Wehrell and Dadswell *unpublished data*). Genetic analysis has identified the aggregation as a mix of individuals from multiple stocks along the east coast of North America, including individuals from U.S. rivers (Wirgin et al. 2012). Since trans-boundary migration is indicated for Atlantic sturgeon, management becomes complex, particularly when mixing of multi-managed individuals occurs. To inform regulatory agencies of areas of importance for the conservation and sustainability of populations of Atlantic sturgeon, it is necessary to better understand their ecology, including diet and composition of essential habitat.

Although the Atlantic sturgeon diet has been studied in freshwater river systems (Vladykov 1948; Guilbard et al. 2007), in the marine environment (Johnson et al. 1997), as well as in estuaries (Haley 1999; Savoy 2007; Guilbard et al. 2007), the diet of the mixed-stock in Minas Basin was unknown. Atlantic sturgeon are primarily benthic feeders which use an inferior placed protrusible mouth to ingest large sections of sediment with a high suction force (Miller 2004). Because much of their time is spent in water with low visibility, particularly in the Bay of Fundy, feeding is done by using a combination of olfactory and taste chemosensory cues, and electroreceptors (Miller 2004). Food habit studies can give us a better understanding of a species major foraging areas, which could help in the protection of essential habitat from adverse human effects (Brosse et al. 2002). The first step in examining food habits is to identify ingested prey

species in all areas of a species habitat. For Atlantic sturgeon, this range includes freshwater river systems, estuaries and coastal marine habitats. It has been suggested that sturgeon feed opportunistically on what is available to them in their immediate surroundings (Johnson et al. 1997; Brosse et al. 2000; Miller 2004; Nilo et al. 2006). If so, there should be a shift in diet composition depending on location and available prey, as well as a diverse diet in areas with high prey diversity and *vice versa*. For example, in the St. Lawrence River estuary, polychaetes and oligochaetes were dominant by number in the diet of 10 sturgeon, whereas in habitats located further upstream in freshwater habitats diets included more insects and amphipods (Guilbard et al. 2007). As far as we know, marine diets usually consist primarily of polychaete worms, followed by isopods, amphipods, and to a lesser extent decapods, shrimp, and small fishes (Johnson et al. 1997; Dadswell 2006). In estuaries such as the Hudson River (Haley 1999) and Connecticut River (Savoy 2007), polychaetes were the dominant prey type followed by isopods and amphipods. An ontogenetic shift in diet has been demonstrated in most sturgeon species up to a certain age; usually small age-0 individuals versus older age classes (Dadswell 1979; Dadswell et al. 1984 a; Muir et al. 1988; Miller 2004). Atlantic sturgeon juveniles (age-0) in the St. Lawrence River were found to feed primarily on gammarids, with older age classes feeding on oligochaetes (Guilbard et al. 2007). This difference in size-class of Atlantic sturgeon and diet composition is likely a factor of foraging location since age-0 sturgeon stay within the freshwater river systems whereas juveniles and sub-adult sturgeon utilize freshwater, estuarine and marine environments (Dadswell 2006).

Diet analyses of other sturgeon species reveal a large portion of prey consumed are soft-bodied organisms. This is particularly the case with lake sturgeon which cohabit the St. Lawrence River estuary with Atlantic sturgeon. A comparison of diet between the sympatric species determined that much of the same prey is consumed, such as gammarids and oligochaetes (Guilbard et al. 2007). The diet of lake sturgeon within the St. Lawrence River estuary, however, was more diverse than that of the Atlantic sturgeon, and included a larger amount of mollusks, including sphaeriid bivalves and gastropods, and even zebra mussels (Guilbard et al. 2007). Other sturgeons appear to consume a higher proportion of prey with harder exoskeletons and even fish. The Gulf sturgeon (*Acipenser oxyrinchus desotoi*), for example, consumes mainly arthropods and annelids, but mollusks have also been found in their diet (Mason and Clugston 1993). The white sturgeon (*Acipenser transmontanus*, McCabe et al. 1993) and the Russian sturgeon (*Acipenser gueldenstaedttii*, Zolotarev et al. 1996) have diets consisting of primarily mollusks, and the shortnose sturgeon (*Acipenser brevirostrum*) feeds heavily on mollusks, changing from clams in more saline portions of estuaries to gastropods in freshwater marshes (Dadswell 1979; Dadswell et al. 1984 a).

In Minas Basin, the extreme tides along with shallow bathymetric gradients create a large intertidal zone (average of 1-2 km wide) that can be used by Atlantic sturgeon to feed at high tide. The foraging strategies of fishes in Minas Basin are of particular interest because the large, semidiurnal tides cause much of the potential foraging habitat to be inaccessible for considerable periods of time and subtidal habitats are often characterized by ledge or heavy gravel deposits. Diet analysis of Atlantic silversides in Minas Basin revealed feeding occurred on the ebb tide only, presumably because their benthic prey

items had been made more accessible during sediment turnover by the turbulent waters of the flooding tide (Gilmurray and Daborn 1981).

The intertidal zone has varying sediment composition, primarily mud or sand that has been eroded from surrounding Triassic sandstone (Bousfield and Leim 1959; Yeo and Risk 1979). The muddy substrate that dominates the northern shoreline of Minas Basin, provides suitable habitat for many benthic organisms, from mud snails (*Ilyanassa obsolete*) to polychaete worms (Westhead 2005). In particular, the larger soft-shell clams, *Mya arenaria,* are commercially exploited in this region. Along the muddy shoreline of the Southern Bight, the finer consistency of the sediment provides favourable habitat to burrowing amphipods, such as *Corophium volutator,* with populations that fluctuate between 20 000- 60 000 individuals/m² (Bousfield and Leim 1959; Percy 2001), and sand-tube building polychaetes such as the bamboo worms (family Maldanidae). This abundance of intertidal prey attracts migrating shorebirds (Hicklin and Smith 1984; Westhead 2005) and bottom-feeding fish, such as the Atlantic sturgeon and flounder (Yeo and Risk 1979). The Southern Bight also supports a groundfish fishery for winter flounder *Pseudopleuronectes americanus* and baitworm harvesting (Westhead 2005). The target of the commercial baitworm harvest is the bloodworm, *Glycera dibranchiata* and large quantities have been exported to the United States for recreational fishing bait since the opening of the fishery in 1985 (DFO 2009 b). Landings of approximately 5 million worms worth $900 000 CAD were reached in 2007 (DFO 2009 b). In Minas Basin, however, *Glycera* populations have decreased with certain areas experiencing serial depletion due to overharvest of potential spawners (DFO 2009 b).

In order to assess the importance of the Minas Basin as a foraging habitat to Atlantic sturgeon, a better understanding of diet is required. The main objective of this study was to identify key species and link physical characteristics of the environments, such as sediment type, to identify components of essential habitat for Atlantic sturgeon in the estuarine/marine environment.

MATERIALS AND METHODS

Study site

Minas Basin, located at the head of the Bay of Fundy, is a shallow estuarine water body known for its large semidiurnal tidal range (mean of 11.5 m; max of 16 m). Minas Basin is separated into four regions: Minas Channel, Central Minas Basin, Cobequid Bay and Southern Bight (Figure 1.1). Much of Minas Basin has depths less than 25 m at low tide, the exception being Minas Channel, with a depth of 115 m (Bousfield and Leim 1959). Vertical mixing in Minas Channel by tidal action causes fairly uniform summer temperatures (14-14.4 ºC) and salinities (31.2-31.4 ‰) throughout the water column causing Minas Channel and Minas Basin to have physical characteristics more similar to a marine environment; whereas Cobequid Bay and the Southern Bight are more estuarine. Two rivers, the Avon and Shubenacadie, flow into the Southern Bight and Cobequid Bay, respectively. In the estuarine areas of both rivers, summer temperatures attained are greater than 20 ºC and salinities are often less than 25 ‰ (Bousfied and Leim 1958).
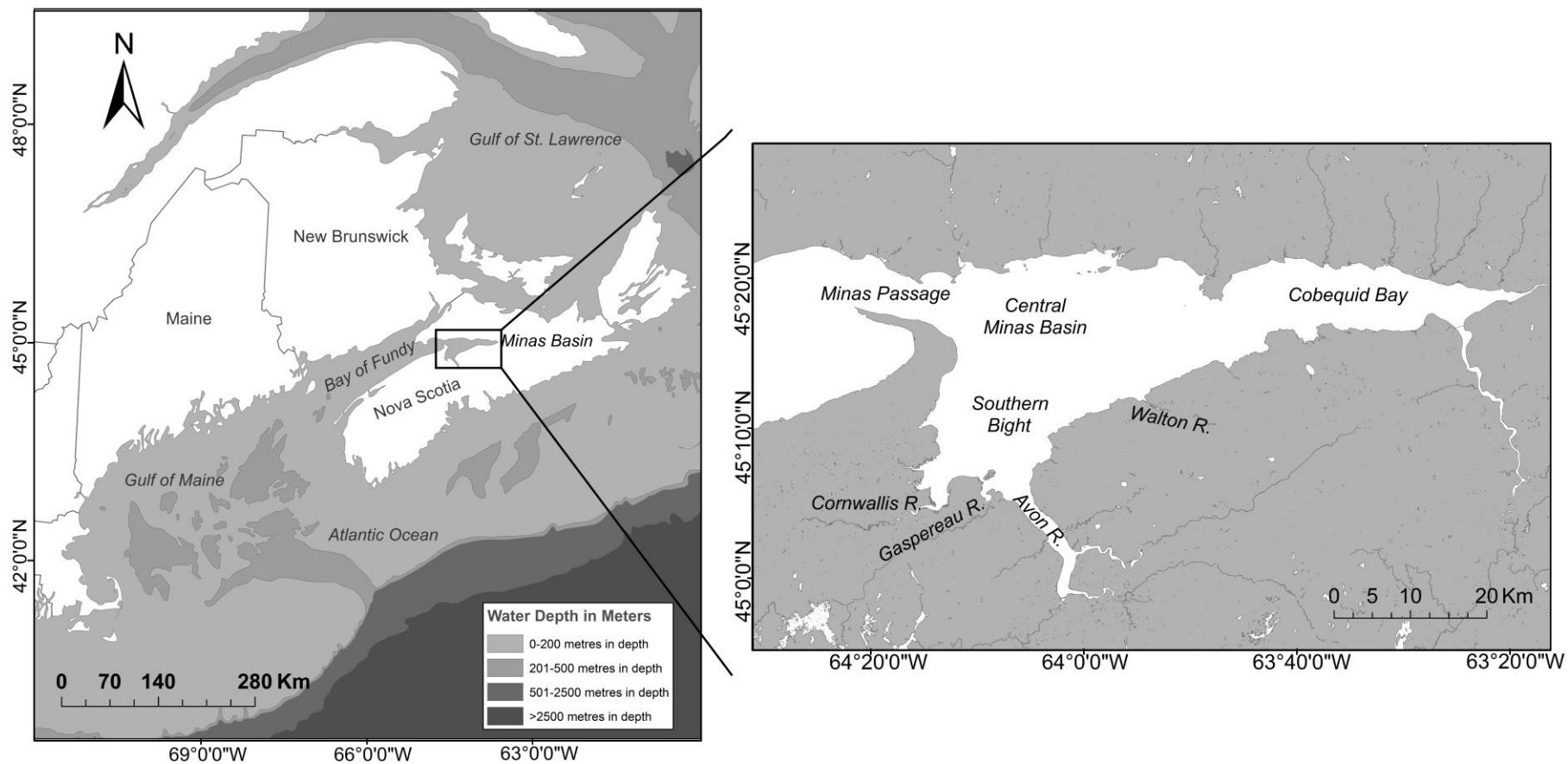
Figure 1.1. The Minas Basin is the north-eastern portion of the Bay of Fundy. It is separated into four distinct regions: Minas Passage, which connects Minas Basin to the rest of the Bay of Fundy, Central Minas Basin, Cobequid Bay, and Southern Bight.

Fish sampling and stomach content analysis

Stomach contents were sampled from Atlantic sturgeon captured during summer (June to August) of 2011 using research directed otter-trawl fishing in the Southern Bight (Figure 1.2). Four trawling expeditions were completed in total at two sites, off Kingsport and Walton. Tow duration was between 40 and 80 minutes at a depth of 5 to 10 metres below the surface, and at a speed of 4 km/h. Benthic tows were conducted using a 24 meter box/trawl net, with a stretch mesh size of 14 cm. The net was equipped with modified rock hopper equipment and 200 kilogram metal doors. Atlantic sturgeon catches ranged from 1 to 12 fish per tow. Fishing was performed under the Department of Fisheries and Oceans Scientific Licence to Fish # 322595. All stomach sampling procedures were performed under Acadia Animal Care Committee protocol # 07-11. Stomach contents were recovered from 21 live specimens ranging from 75.5 to 155.5 cm FL (Figure 1.3) during trawling operations using a revised gastric lavage technique (Brosse et al. 2002).

Most of the collected prey were live during removal, thus we can assume they were recently consumed. After collection samples were immediately preserved in 5% formalin. Samples were sorted, classified and enumerated in the lab. Taxonomic identification was done using keys by Appy et al. (1980) and Bromley and Bleakney (1984). Differences among sample variables such as sturgeon fork length, wet weight of contents produced, and number and weight of prey per sample were described ($\overline{x} \pm SD$).
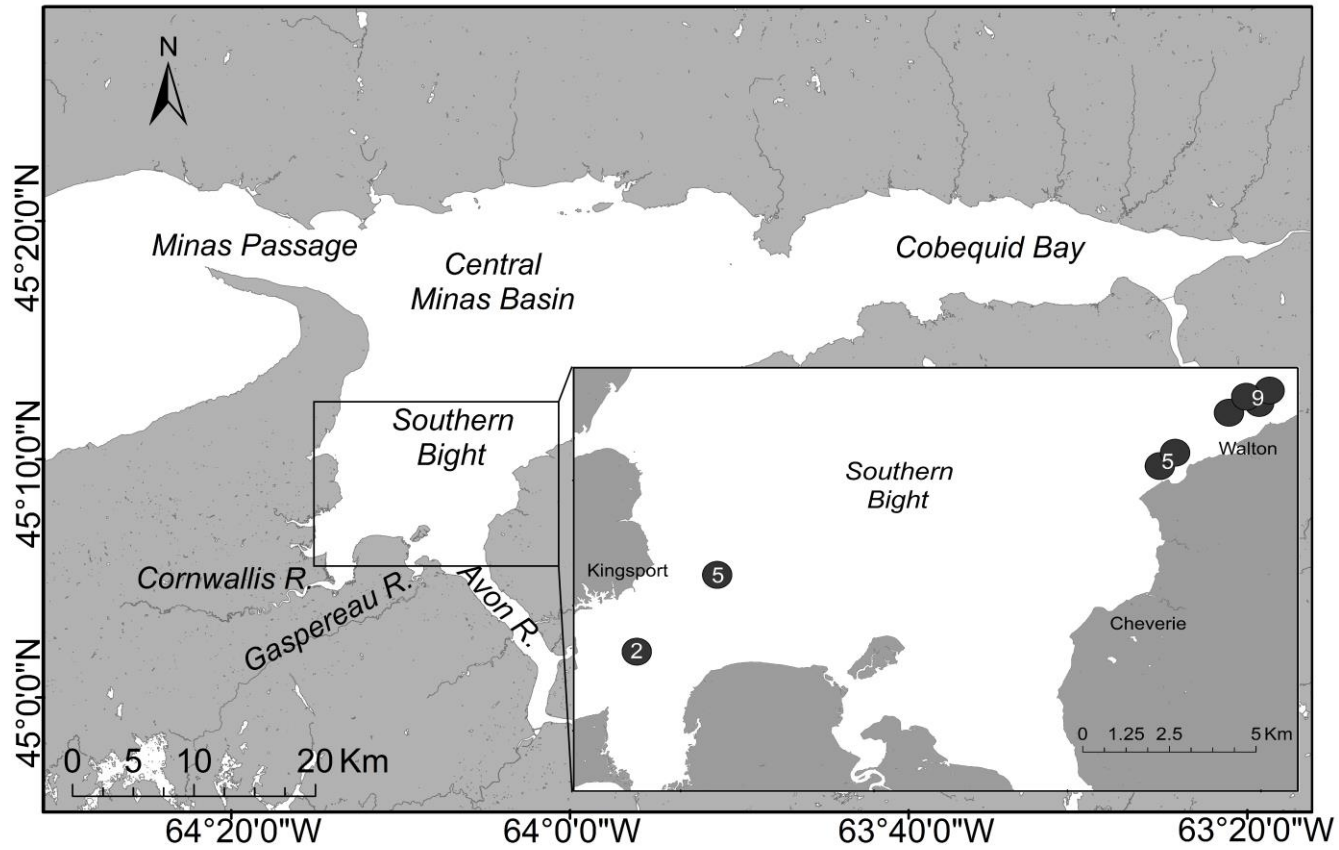
Figure 1.2. Atlantic sturgeon were captured by directed otter-trawls carried out in several locations within the Southern Bight, Minas

Basin. Inset indicates the number of individuals sampled at each trawl location for a total sample size of 21.
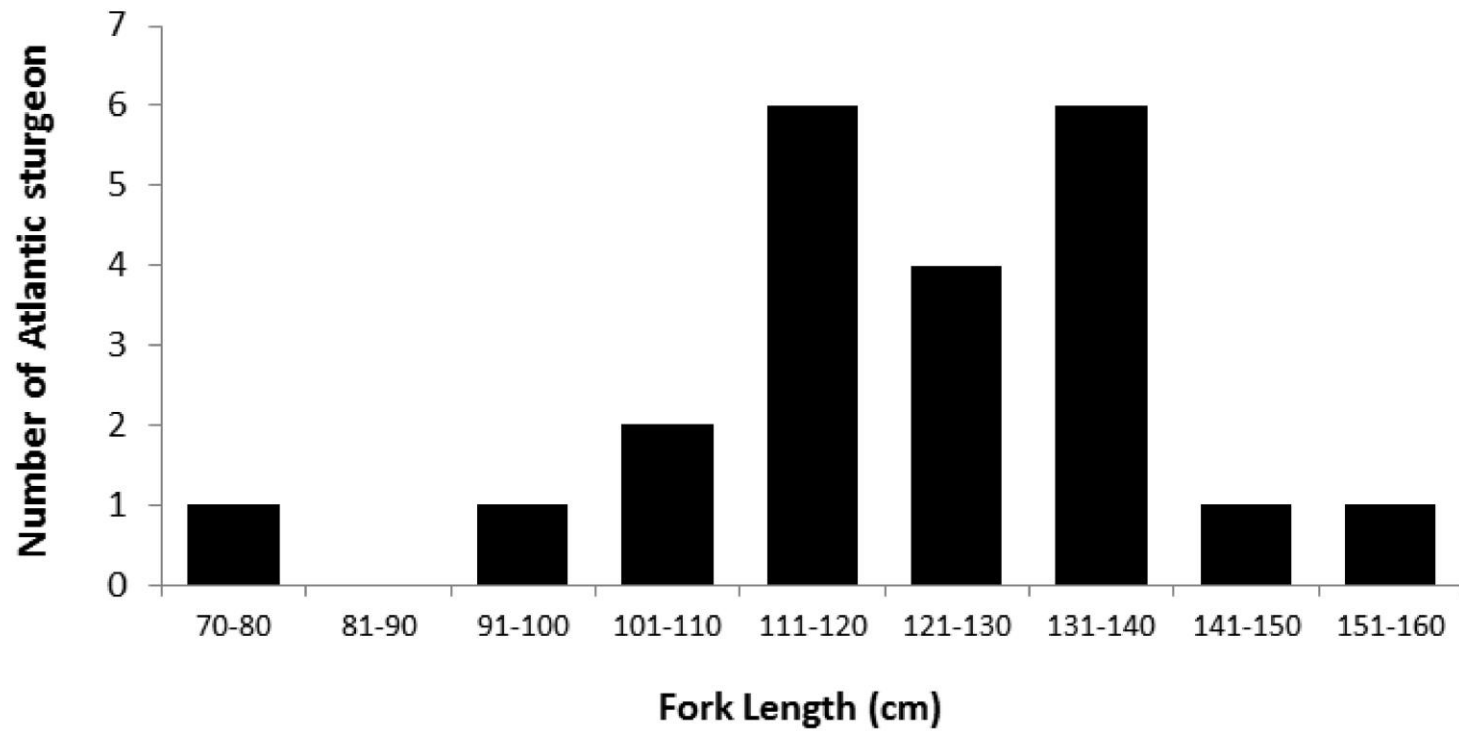
Figure 1.3. Length-frequency of all sampled Atlantic sturgeon (n = 21) captured by otter trawl in Minas Basin, Bay of Fundy during summer 2011.

Figure 1.4. A 2-L pressurized water tank was attached to a medical-grade catheter which was carefully maneuvered down the sturgeon oesophagus until it reached the hind portion of the stomach. Continuous bursts of water forced food from the stomach back out through the mouth. Individual in photograph was 92 cm FL.

Adult Atlantic sturgeon are known to feed on prey of multiple taxa ranging in size (from 0.1 – 10 cm) and in various numbers per prey item (Hoover et al. 2007; Guilbard et al. 2007; Nellis et al. 2007). Therefore, to represent the importance of different prey items to the individual diets of sampled sturgeons, items were separated by taxa and pooled. Percent occurrence (%O), percent mean relative abundance (%N), and percent weight

(%W) were determined for prey items by taxon. The diet of an individual was quantified using the index of relative importance (IRI) calculated for each taxon, excluding vegetal matter. The IRI can be defined as:

$$IRI = (N + W) * O$$

Where N is the percent number of certain prey item, W is the percent weight and O is the frequency of occurrence (Kurian 1977; Hyslop 1980). Empty stomachs were excluded from this analysis.

The number of prey items consumed in relation to size of fish was examined using a univariate analysis of variance (ANOVA). The relationship between number of prey taxa consumed and size of fish was also examined using an ANOVA.

The degree of gut fullness was calculated using Hureau's index Ir (Berg, 1979), where:

$$Ir = ingested\ biomass/body\ weight\ x\ 100\%$$

Because of the extreme tides in Minas Basin, the degree of gut fullness and relationship to tidal state and time of day were also examined (Gilmurray and Daborn 1981). Gut fullness was compared between the two main capture locations (Figure 1.2).

A Shapiro-Wilk test for Ir normality revealed a non-normal distribution. Thus correlation coefficients were determined using the non-parametric Mann-Whitney U-test for fullness index in relation to both tidal state and capture location. In addition, a Kruskall-Wallis rank sum test was used to examine gut fullness during various times of the day (morning, mid-day, and evening). To examine fish size and gut fullness, Ir values were log transformed and an ANOVA was used to test the transformed data. Alpha level

of 0.05 was used for all tests. All statistical analyses were conducted using R

programming interface (R Development Core Team 2010).

RESULTS

Of the 21 Atlantic sturgeon stomachs sampled, one was empty (no organic or

inorganic material). Sand and organic debris was minimal across most samples (<0.01 g),

and was excluded from further analysis. Overall, polychaetes were the major prey class

consumed and contributed more to the diet in occurrence, abundance and weight (Figure

1.5).

Major taxa consumed by Atlantic sturgeon, as determined by the IRI, were the

polychaetes, *Clymanella* sp. and *Spiophanes bombyx.* Other polychaetes present were

Eteone sp., primarily *Eteone trilineata* and *Eteone longa*, *Nephyts* sp., Neireididae sp.,

and Glyceridae sp., including the bloodworm, *Glycera dibranchiata*. Crustaceans,

including *Corophium* sp. and mysids such as, *Neomysis americanus,* occurred minimally

in the Atlantic sturgeon diet. Other species identified in trace amounts included the sand

shrimp *Crangon septemspinosa*, the isopod *Chiridotea coeca*, the amphipod *Unciola*

irrorata, and an unidentified species of Cumacean (all <0.01%). Trace amounts of fish

scales were present in 5 of the stomach samples; however, no other identifiable body

parts accompanied the scales. Thus they were considered organic debris and not a

primary component of the sturgeon diet.

Only two stomachs contained notable amounts of other benthic matter. Witch's

hair kelp, *Desmarestia aculeata,* comprised a third of the wet mass in one sample (ID

2626), but it was still not the most abundant item consumed. The hydroid, *Abietinaria*

abietina, was identified in another gut sample (ID 2629). This particular sample also contained the only notable amounts of organic debris and sand, comprising 50% of the sample wet weight.

There was no significant difference in the number of prey items consumed and fork length of the fish ($F = 2.39$, $df = 19$, $P = 0.14$), nor number of prey taxa consumed and fork length ($F = 1.14$, $df = 19$, $P = 0.30$). Gut fullness was also not significantly related to size of fish ($F = 4.12$, $df = 18$, $P = 0.06$).

There was no significant difference in gut fullness between the two capture locations in the Southern Bight (mean ranks for Kingsport and Walton were 19 and 10, respectively; $U = 63$, $Z = 1.04$, $p > 0.05$, $r = 0.23$), or time of day the stomachs were sampled at (Kruskall-Wallis Chi ^{2} = 2.51, $df = 2$, $P = 0.28$). When tide stage was examined, gut fullness was higher on the ebb tide (median $\pm$ SD; $Ir = 0.05 \pm 0.14$) than the flood tide (0.03 ± 0.03), however this difference was not significant (mean ranks for ebb and flood were 13.81 and 9.18, respectively; $U = 35$, $Z = 1.41$, $p > 0.05$, $r = 0.31$).
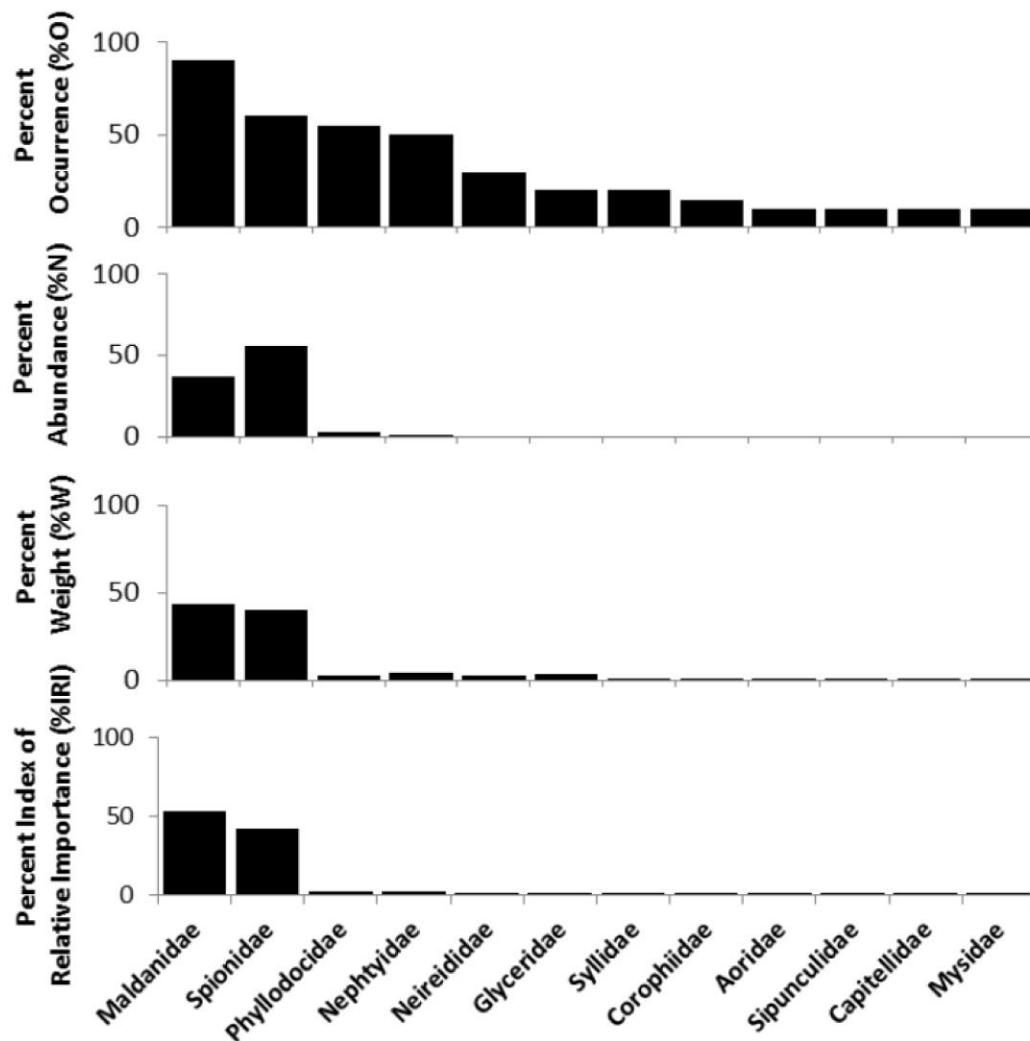
Figure 1.5. Relative occurrence (%O), abundance (%N), and weight (%W) of taxa

collected from the stomach contents of sub-adult and adult Atlantic sturgeon (n = 20)

captured by trawling during summer 2011 in Minas Basin, Bay of Fundy. The percent

index of relative importance (%IRI) of each taxa to the sturgeon diet is also presented.

IRI is defined as: (N + W) * O. Prey taxa with %O < 10 were not included but the

following: Goniadidae, Pyramidellidae, Scalibregmatidae, Oithonidae, Idoteidae,

Diastyidae, Crangonidae, Arenicolidae, Tomopteridae, Gammaridae, and Paraonidae

were recovered.

DISCUSSION

Atlantic sturgeon diets in Minas Basin consisted almost exclusively of polychaetes (99.7% IRI). Samples were dominated by families Maldanidae (the bamboo worms), and Spionidae, primarily the species *Spiophanes bombyx*, both abundant sand-tube dwelling invertebrates in the Minas Basin intertidal mudflats (Glenys Gibson *unpublished data*). Atlantic sturgeon are commonly found close to coastlines and within proximity to coastal features such as bays and inlets, and tend to prefer sandy bottom types within a depth of less than 65 m (Stein et al. 2004). Sediment mapping of intertidal mudflats in the Southern Bight by Hicklin and Smith (1984) showed that silt and clay were the primary grain size of 67% of sample sites, with the remaining sites consisting of larger sediments, such as sand. They reported polychaete densities were negatively correlated with finer grain size and were more abundant in areas with coarse-medium sand (Hicklin and Smith 1984). Although gut samples in this study were from sturgeon collected from various areas in the Southern Bight an overall preference toward intertidal sand tube-dwelling polychaetes was evident.

Acoustic tracking of Gulf sturgeon revealed that 63.8% of occupied space in the coastal marine environment was over coarse sand and shell fragment bottom type, and only 8.5% was over mud/silt-clay or fine sand/mud (Ross et al. 2008). Fox et al. (2002) and Harris et al. (2005) also found Gulf sturgeon to have a high association with sand substrata. This makes sense as sturgeon can intake large quantities of sediment during feeding. Lack of sediment within sturgeon gut samples in this study indicates that most sediment is flushed through the gills and prey items are sieved out and pass through the digestive tract (Miller 2004). Perhaps selection toward sediment with larger, less compact

particles may make this process more gentle on gill filaments, and less likely to clog them than finer silt and clay.

Generally, diet analysis revealed that Atlantic sturgeon are opportunistic benthic predators that show a preference for polychaetes, as stomach contents indicated the presence of burrowing polychaetes and other bottom-dwelling invertebrates. Previous studies on Atlantic sturgeon food habits demonstrated a shift in diet depending on its local environment and prey availability. Vladykov (1948) found that Atlantic sturgeon residing in the freshwater part of the St. Lawrence estuary fed on insect larvae, crustaceans, and worms, whereas sturgeon collected in the mesohaline portion of the estuary preyed mainly on polychaetes. An ontogenetic shift in diet is commonly recognized in Atlantic sturgeon with diet diversity increasing with the size of the fish (Guilbard et al. 2007). We detected no significant difference in size of fish and number of prey items nor number of prey taxa consumed in this study, however this result may be a factor of our limited sample size. Sampled sturgeon were between 75.5 to 155.5 cm FL and represent the sub-adult/adult age-classes so comparisons with younger juveniles could not be done, which is often where differences in diet are identified (Dadswell 1979; Muir et al. 1988; Miller 2004; Guilbard et al. 2007).

There was no significant difference between gut fullness and tidal stage which may indicate that foraging is occurring during all phases of the tide. Slightly higher gut fullness was recognized on the ebb tide, which is similar to what was found for Atlantic silversides in Minas Basin (Gilmurray and Daborn 1986). Recently, Atlantic sturgeon movements over the Minas Basin intertidal zone were described (McLean et al. 2013 *in review*). Data revealed that acoustically tagged Atlantic sturgeon followed the incoming

tide and that foraging and searching behaviours continued over the duration of the tide until the fish were forced back into deeper water at low tide (McLean et al. 2013 *in review*). Atlantic sturgeon were captured by trawl in deeper waters so it is difficult to identify exactly when they were foraging, however, because their preferential prey were intertidal polychaete worms, it is likely they ceased feeding during low tide when the mudflats were completely exposed.

Lack of sand and organic debris in the gut samples is quite unique in the scientific literature. For example, substantial amounts of sand and organic debris were noted in the stomachs of Atlantic sturgeon in the St. Lawrence River (Vladykov 1948). Johnson et al (1997) also found that it comprised an average of 42.5%, by weight, of Atlantic sturgeon stomach samples off the coast of New Jersey. Similarly, large quantities of plant matter was infrequently consumed by sturgeon in Minas Basin. Most Atlantic sturgeon are thought to ingest organic material and inorganic detritus incidentally during the feeding process. Vegetal matter is common in many studies, sometimes reaching 50% occurrence in near-shore samples (Guilbard et al. 2007). Overall conclusive evidence is lacking on whether organic material plays a role in the dietary requirements of sturgeons (Smith 1985; Mason and Clugston 1993), however it has been suggested that digestible biofilm and substances extracted from the vegetal matter could constitute an additional nutritional source for the consumer (Mason and Clugston 1993). Detritus and organic material was present in trace amounts in all Atlantic sturgeon stomach samples in this study, with one of these containing notable amounts of plant material. It is possible that plant material and detritus were not successfully retrieved during the sampling period, but I assume this was not the case. Rather the limited plant matter in the intertidal zone of Minas Basin

(Percy 2001), particularly in areas where tube-dwelling polychaetes are most abundant, is a more likely explanation for low presence in our samples.

Digestion rates are poorly understood for sturgeons (Mason and Clugston 1993; Johnson et al. 1997), thus it is possible that some digestion of prey occurred before preservation causing an underrepresentation of soft body taxa. Because, however, much of the prey items retrieved using the gastric lavage technique were still living, we can assume that most items were recently consumed and thus represent an accurate overview of their diet. Perhaps an underrepresentation of larger or harder prey items occurred due to the method of food extraction. Pulsed water was efficient in retrieving small soft organisms that could be moved around by the water pressure, however hard pieces of shell or bone may not have been able to pass through constricted alimentary canals and were therefore missed during the extraction process (Wanner 2006).

Atlantic sturgeon diets are generally less diverse than other species, in part due to frequent foraging in estuarine environments where available prey items are less diverse than freshwater or marine ecosystems (Guilbard et al. 2007). In Minas Basin, Atlantic sturgeon fed on 23 taxa, which is just slightly higher in diversity than other studies. Only 12 of the reported taxa, however, had greater than 10% occurrence, suggesting that fewer than 23 are actually important to the overall diet. In other estuarine systems, 14 benthic families were identified by Vladykov (1948), 15 by Nellis et al. (2007) and 10 by Guilbard et al. (2007). Similarly low taxa diversity was found in the stomach contents of Atlantic sturgeon in the Hudson and Suwanne River estuaries (Haley 1999; Mason and Clugston 1993).

The Atlantic sturgeon is apparently an opportunistic predator of sandy and silty mudflats, utilizing much of the available prey located within the intertidal region of Minas Basin. The total dominance of polychaetes in this location is likely one of the more important considerations for future management plans. In this study, bloodworms comprised a considerable portion of the diet by weight (10%) for a single taxa, suggesting that baitworm harvest could deplete the available prey for sturgeon consumers. Future studies should focus on the caloric value of each prey item in order to fully evaluate prey importance to the Atlantic sturgeon diet as well as to better estimate the potential effects of direct competition for baitworms with harvesters.

ACKNOWLEDGEMENTS

CHAPTER 2

QUANTIFYING MOVEMENT PATTERNS OF ATLANTIC

STURGEON IN THE MINAS BASIN, BAY OF FUNDY

ABSTRACT

Quantifying animal movements can reveal spatial and temporal patterns of habitat use and may improve our understanding of the foraging strategies of marine predators where direct observations of feeding behaviour are rare or impossible because of turbidity. Fine-scale movement data from 25 acoustically tagged Atlantic sturgeon was gathered using a Vemco Positioning System (VPS) array of hydroacoustic receivers in the intertidal zone of Minas Basin, Bay of Fundy, during summer 2011. From these data sturgeon relocations and movement trajectories were determined. Sturgeon movement trajectories were categorized into three movement types by analyzing four calculated metric variables including: 1) mean distance between successive relocations; 2) mean relative angle or "turning angle"; 3) mean rate of movement (ROM; m/s); and 4) a linearity ratio. Movement Type 1 trajectories were characteristically slow and winding, with short steps between relocation, whereas Movement Type 2 were fast and tortuous. Movement Type 3 trajectories were fast and linear, with large steps between relocations. Considerable variability in movement type was recognized with 11 individuals performing all three types of movement during the monitoring period. Movement Types 1 and 2 occurred primarily over the intertidal zone where sediment type was comprised of larger sand and sandy/silt particles. This association with larger grain size coincides with a diet preference of sand-tube dwelling polychaetes and confirms the importance of the intertidal zone to foraging Atlantic sturgeon. All movement types were equally likely to occur throughout a 24-hour day and throughout all tidal stages, however there was higher overall crepuscular activity which revealed a temporal pattern not previously recognized for adult Atlantic sturgeon.

INTRODUCTION

Recent advances in acoustic telemetry technology allow simultaneous monitoring of multiple individuals during short temporal periods (Heupel et al. 2004) and permit researchers to answer questions relevant to fisheries management. Acoustic telemetry can also be used to test hypotheses important to the development of conservation strategies for near-threatened (Moser and Lindley 2007, Lindley et al. 2008), threatened (Fox et al. 2000) or endangered species (Hissmann et al. 2000, Welch et al. 2009, Simpfendorfer et al. 2010), including information about their life histories (Lindley et al. 2008). By studying an animal's movements, behavioural and ecological processes, such as navigation, migration, dispersal, space use and food searching (Benhamou 2004), fundamental to their overall survival and fitness can be determined.

Habitat use has commonly been described by spatial distribution through the use of kernel utilization densities and convex polygons to estimate activity space (Heupel et al. 2004; Collins et al. 2007; Yeiser et al. 2008), and/or residency times (Holland et al. 1993; Collins et al. 2007), however, these data are not often used to examine the underlying behavioural patterns demonstrated by such movements. Fine-scale spatial and temporal movement data provided by electronic tags has been used to classify animal movement into various behavioural categories such as foraging versus migratory or transitory (Austin et al. 2004; Jonsen et al. 2007; Bailey et al. 2008; Heupel et al. 2012). The trajectory of an animal track, or curve recoded by a tagged animal when it moves, can be analyzed to segregate these recorded behaviours (Calenge 2011). The tortuosity versus linearity of a curve can further be assessed in order to categorize behaviour (Benhamou 2004; Heupel et al. 2012). During foraging, animal movements tend to be

more tortuous in nature, with smaller turn angles and less time between subsequent relocations or steps (Benhamou 2004). Recently, behavioural patterns of some species have been examined using the Vemco Positioning System (VPS) that provides fine-scale data on animals carrying acoustic telemetry tags moving through a dense array of hydroacoustic receivers (Espinoza et al. 2011 a,b; Reubens et al. 2011; Farrugia et al. 2011). This research has focused on determining how physical variables (i.e. bathymetry, temperature, salinity) related to habitat utilization of tagged fishes (Reubens et al. 2011; Dean et al. 2012; Middel et al. 2012). The determination of species-specific characteristics of movement is central to determining how animals use areas and therefore what areas may be most important to protect.

Atlantic sturgeon are a long-lived, slow growing species that historically supported a commercial fishery in the U.S. (Vladykov and Greeley 1963; ASMFC 1998). Overharvesting at the turn of the 19th century, coupled with habitat degradation, pollution and loss of suitable spawning habitat caused extirpation in some rivers (Dadswell 2006), and in response the U.S. declared a fishing moratorium on Atlantic sturgeon in 1997 (ASMFC 1998). More recently, four of the five distinct population segments of Atlantic sturgeon along the eastern U.S. were listed as 'endangered' and one as 'threatened' under the ESA (NOAA 2012 a,b). In Canada, there are two known spawning populations located in the Saint John River, New Brunswick and St. Lawrence River, Quebec. In 2011 the Saint John River population was listed as threatened by COSEWIC under SARA (COSEWIC 2011). Both the Saint John River and St. Lawrence River populations, however, continue to support commercial fisheries for Atlantic sturgeon (DFO 2012).

Coastal migrations are common for sub-adult and adult Atlantic sturgeon and a certain degree of mixing between the stocks has occurred at foraging sites (Wirgin et al. 2012). During the summer months the Minas Basin, Bay of Fundy is a terminus for approximately 9 000 to 10 000 migrating Atlantic sturgeon (Wehrell and Dadswell *unpublished data*). Acoustic telemetry has been used to attempt to determine stock structure and migration patterns for Atlantic sturgeon over much of their range from the St. Lawrence estuary, Quebec in the North to southern parts of Georgia in the U.S. in the south (Moser and Ross 1995; Collins et al. 2000; Hatin et al. 2007; Fernandes et al. 2010; Fox and Breece 2010; Erickson et al. 2011). Atlantic sturgeon seasonal movements have been described to and from spawning rivers (Collins et al. 2000; Hatin et al. 2007), overwintering sites (Erickson et al. 2011) and feeding grounds (Kieffer and Kynard 1993). Although research is extensive, none of these studies have quantified the behavioural traits underlying the observed movements. This study had three overall objectives. The first objective was to develop a procedure to quantify Atlantic sturgeon movement in the intertidal regions so that behaviours indicative of feeding could be identified. The second objective was to define the relationship between movement behaviours and the tidal and diurnal cycles. Tidal and diurnal cycles may be time varying drivers of behaviour whose influence needs to be understood to put movement behaviours in context both spatially and temporally. The third and final objective was to link foraging behaviour with sediment type. Taken together, these objectives have allowed us to gain a better understanding of the biotic and physical drivers of sturgeon behaviour.

MATERIALS AND METHODS

Study site

Atlantic sturgeon movements were examined in the tidal region of Kingsport Beach, Minas Basin (Figure 2.1). Minas Basin is a shallow estuarine water body connected to the Bay of Fundy by Minas Passage through which large amounts of water (> 10 cubic kilometers, or 10 billion tons) transit the system during each phase of the semi-diurnal tides.

Average tidal amplitude is 11.5 m with some amplitudes surpassing 16 m on spring tides (Bousfield and Leim 1959). Much of the Minas Basin has a depth less than 25 m at low tide, with the exception of the Minas Passage which reaches depths up to 115 m (Bousfield and Leim 1959; Percy 2001). Minas Basin and Minas Passage experience vertical mixing by the tides causing uniform temperatures and salinities (Bousfield and Leim 1959). These physical characteristics and extreme tides along with shallow bathymetric gradients create a 1-2 km wide intertidal zone with varying sediment composition (Yeo and Risk 1981). Kingsport intertidal was chosen for VPS placement because it is a locally known aggregation site for Atlantic sturgeon during the summer and it is accessible by foot and by boat.

Field methods

A total of eighty-three Atlantic sturgeon were captured by weir and directed otter-trawl during the summer months (June to August) of 2010 and 2011. Transmitters (V16, 16 mm x 65 mm, Vemco Ltd., Nova Scotia) were surgically implanted into the abdominal cavity. Fishing was performed under the Department of Fisheries and Oceans Scientific Licence to Fish # 322595. Tagging procedures were performed under Acadia Animal

Care Committee protocol # 07-11. To facilitate transmitter insertion a large PVC cradle capped on one end was tipped at a 45 angle to allow water to pool. A stock solution of 10 mg/L of MS222 was mixed with 20 L of fresh seawater and poured into the PVC cradle. Atlantic sturgeon were placed dorsal side up with their head and gills fully submerged in the anaesthesia bath until opercular beats were slowed and they were unresponsive to gentle stimulus such as a tail grab. Anaesthetised sturgeon were removed from the bath and placed ventral side up on a moistened tarpaulin. A 3-4 cm incision was made on the ventral surface on either side of the *linea alba*; generally posterior to the pelvic girdle. Transmitters (Table 2.1) were inserted and pushed approximately 4 cm anteriorly using the tip of a blunt probe.

Two horizontal mattress sutures, using sterile absorbable 1/0 Ethilon monofilament nylon sutures with a reverse cutting edge (Johnson & Johnson, Ontario), were used to close the incision site. All equipment, including transmitters, was disinfected prior to surgery using a 10% Betadine solution, followed by a saline rinse. Surgeries lasted 2-4 minutes excluding anaesthesia and recovery time. Post-surgery, sturgeon were held in a recovery tank and allowed sufficient time for the anaesthesia to wear off and for their condition to be monitored before being released in an area near the capture site. All sturgeon were also marked with an external dart tag (FLOY) and internal Passive Integrated Transponder tags (PIT) for identification purposes, measured to the nearest fork length in cm, weighed to the nearest g and sampled for DNA prior to release.
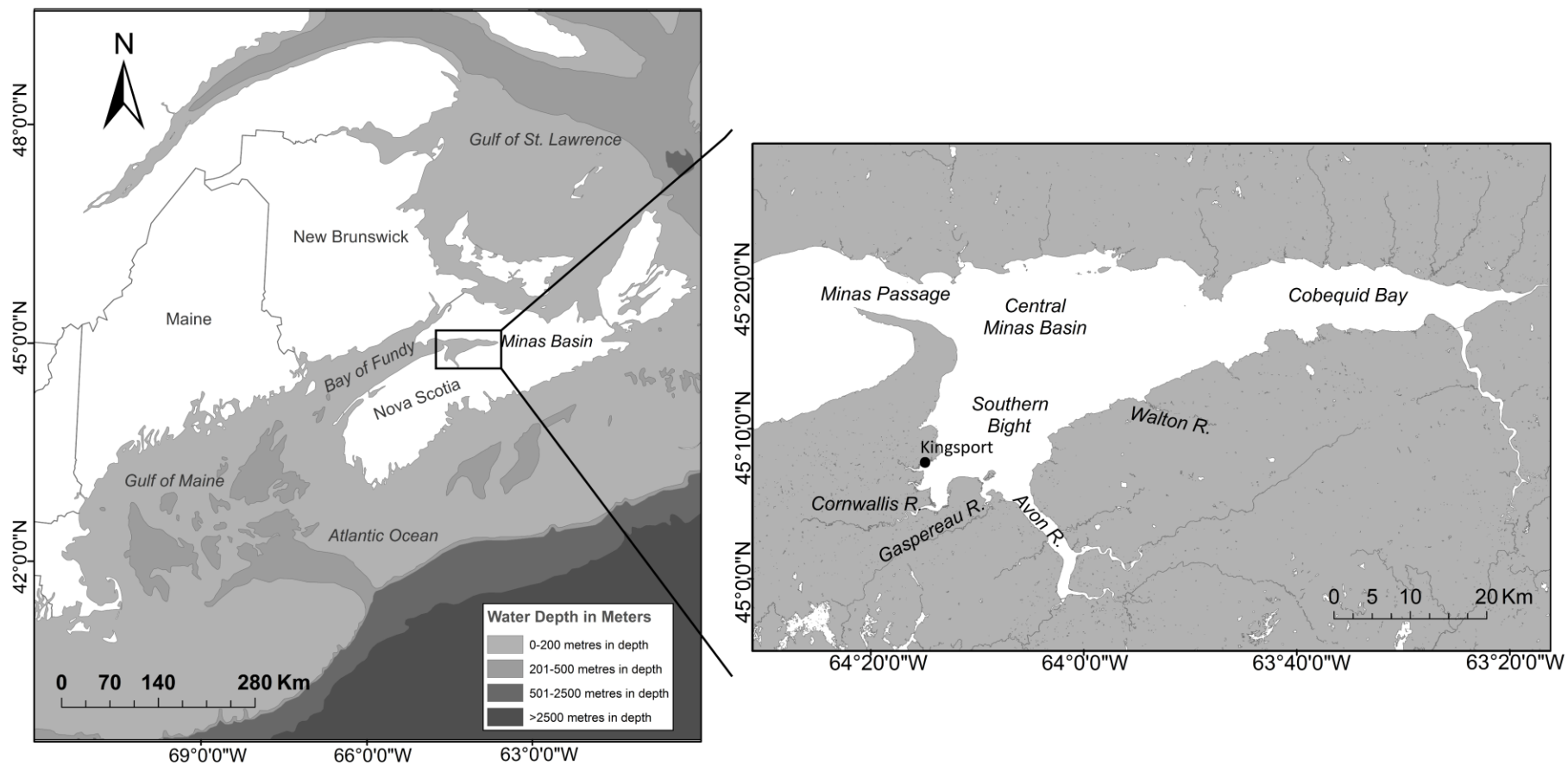
Figure 2.1. The Minas Basin is the northern most portion of the Bay of Fundy. It is separated into four distinct regions, including:

Minas Passage, which connects Minas Basin to the rest of the Bay of Fundy, Minas Basin, Cobequid Bay, and Southern Bight.

Table 2.1. Coded acoustic tag models used during Atlantic sturgeon tagging project in Minas Basin during summers of 2010 and 2011 (n = 83). All models supplied by Vemco/Amirix , Inc., Halifax, NS, Canada.

Tag model	Year	Number used during study	Dimensions (mm)	Weight in air (g)	Battery life (days)	Power output (dB)
V16-6x	2010	17	16 x 95	34	1633	160
V16P-6x*	2010	8	16 x 98	36	1287	160
	2011	53				
V16TP-6x*	2010	5	16 x 98	36	1609	160

Note *tag includes environmental sensor (i.e., pressure and/or temperature)

Upon release, the presence and movements of acoustically tagged sturgeon were monitored using a gridded array of 15 VR2W omnidirectional acoustic receivers (Vemco Ltd, Nova Scotia) with overlapping detection ranges deployed on Kingsport Beach (Figure 2.2). Units were moored on steel rebar posts and deployed at low tide so they could be secured into sediment to prevent drifting and GPS coordinates of exact locations were recorded. Units were deployed so the hydrophone was 45 cm above the sediment. Three temperature and pressure tags (V16TP-6X, 69 kHz), with nominal code transmission delays of 900 s (600 – 1200 s), were stationed throughout the acoustic array to measure thermal gradients and water level (Figure 2.2).
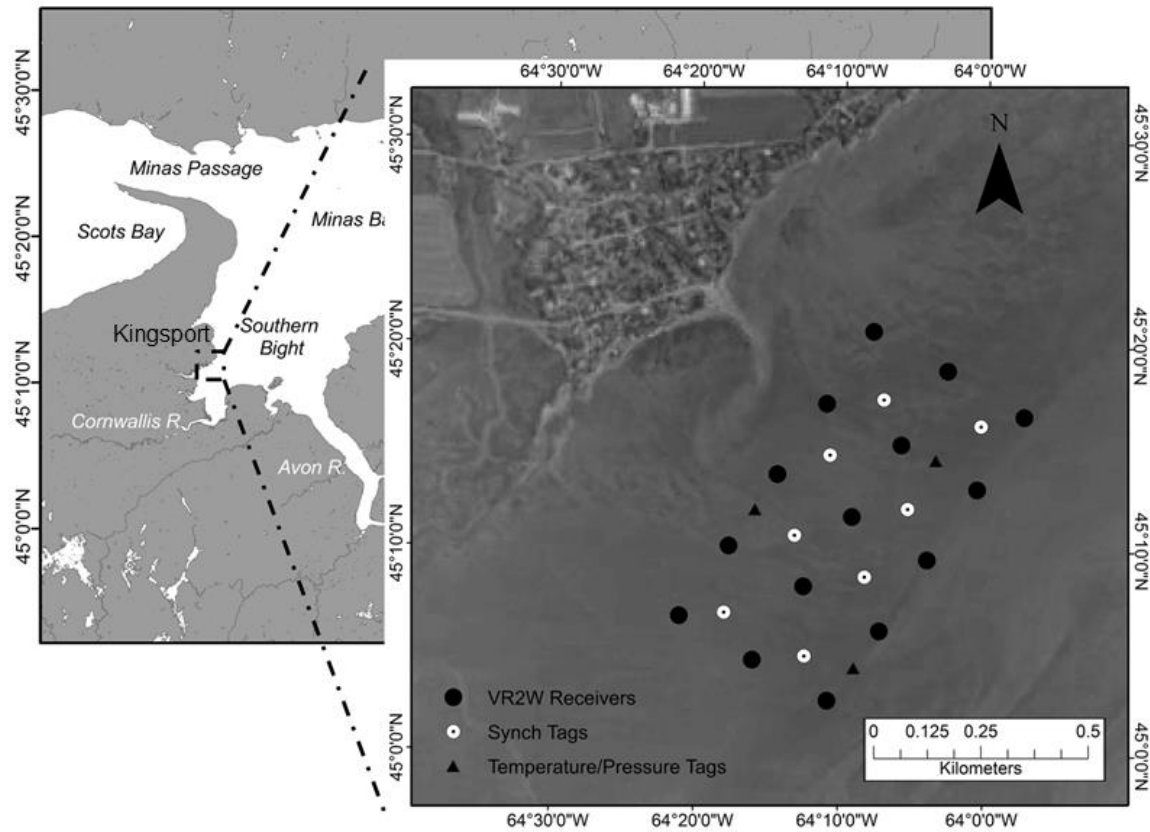
Figure 2.2. A Vemco Positioning System array was deployed at Kingsport Beach, in the Southern Bight of Minas Basin, to examine fine-scale movement behaviour of acoustically tagged Atlantic sturgeon. The array consisted of 15 VR2W receivers, 8 synchronization tags, and 3 temperature and pressure sensor tags.

Eight synchronizing transmitters or "sync tags" (Vemco 16-6X, 69 kHz) with a nominal code transmission delay of 60 seconds (range 30 – 90 s) were also deployed within the array to correct for internal clock drift and therefore synchronize the internal clocks of receivers at the post-retrieval stage (Figure 2.2). Sync tags were placed <100 m from each receiver to ensure the best possible time synchronization (Espinoza et al. 2011 a,b). The VPS of acoustic tags and sync tags allowed triangulation of an individual through the use of differences in detection arrival times at three or more receivers.

Vemco VPS Software (Vemco, Ltd, Nova Scotia) was used to analyze VPS and Horizontal Position Error (HPE) data. The HPE is the estimated error associated with each calculated position (Espinoza et al. 2011 a). Data were classified according to tidal state (flood, ebb, low water, high water, and mid-water/slack) and diel stage (day, night). Accurate tide tables supplied by the Government of Canada (www.waterlevels.gc.ca) were used for high and low tide times. Sunrise/sunset data were obtained from the National Research Council Canada for the Halifax region (http://www.nrc-cnrc.gc.ca/eng/services /hia/ sunrise-sunset.html).

Trajectory analysis

To assess fine-scale movement patterns of tagged Atlantic sturgeon, a HPE filter of < 50 m was used. Locations with > 50 m HPE were removed using a filter for trajectory analysis which was carried out using the *adehabitatLT* package (Calenge 2011) in R (R Development Core Team 2010). Because many individuals were present within the array on a number of occasions, trajectories were categorized into "bursts" based on date and time of detection. Doing this gave each "burst" an associated time stamp which allowed for further analysis. A maximum of 6 hours was used because the semi-diurnal

tides in the area would likely displace the animal at low tide (i.e. would not be detected).

Only "bursts" with > 5 relocations were used for trajectory assessment. Trajectories were

described using four measured variables: 1) the distance between successive relocations;

2) rate of movement (ROM; m/s); 3) the relative angle or "turning angle" which measures

the change in direction between relocations, as defined by Calenge et al. (2009) and

Calenge (2011); and 4) a linearity ratio. Linearity ratios were established for each "burst"

by calculating the distance between steps and dividing by the total distance (sum of each

of the steps) where values approaching 1 indicated linear movement and values

approaching 0 indicated tortuous movement (Heupel et al. 2012). Central tendencies

(mean) and dispersion values (standard deviation, SD) were also calculated for all

variables, excluding linearity ratios. A correlation matrix plot was produced using the R

package *corrplot* (Wei 2012) and strongly correlated variables (>30% correlation) were

removed from further analysis. A within group sum of squares plot was used to identify

three clusters in the trajectory data set (Figure 2.3). A k-means cluster analysis was used

to partition bursts into one of the three identified clusters (Figure 2.4). Cluster analysis

was done using the R (R Development Core Team 2010) package *cluster* (Maechler et al.

2002). Clusters were henceforth referred to as Movement Type 1, Movement Type 2, and

Movement Type 3. Univariate analyses of variance (ANOVA) were used to test for the

significance of each of the metric variables in characterizing sturgeon trajectories.

Tukey's honestly significant difference (HSD) post hoc test was used on significant tests

to identify the source of any variation.

An ANOVA was used to test for significant differences in type of movement

performed by tagged sturgeon and time of day. Qualitative data was recorded for each

movement type based on water level (i.e. high, mid, and low water levels) and tidal stage (i.e. flood and ebb) at the time the movement was performed. An ANOVA was used to test for significant differences between movement type and mean tide level. In addition, ANOVAs tested for significant differences in when each movement type began and ended in relation to water level. Chi-square contingency tests were employed to determine any significance in the proportions of movement type between water level and tidal stage.
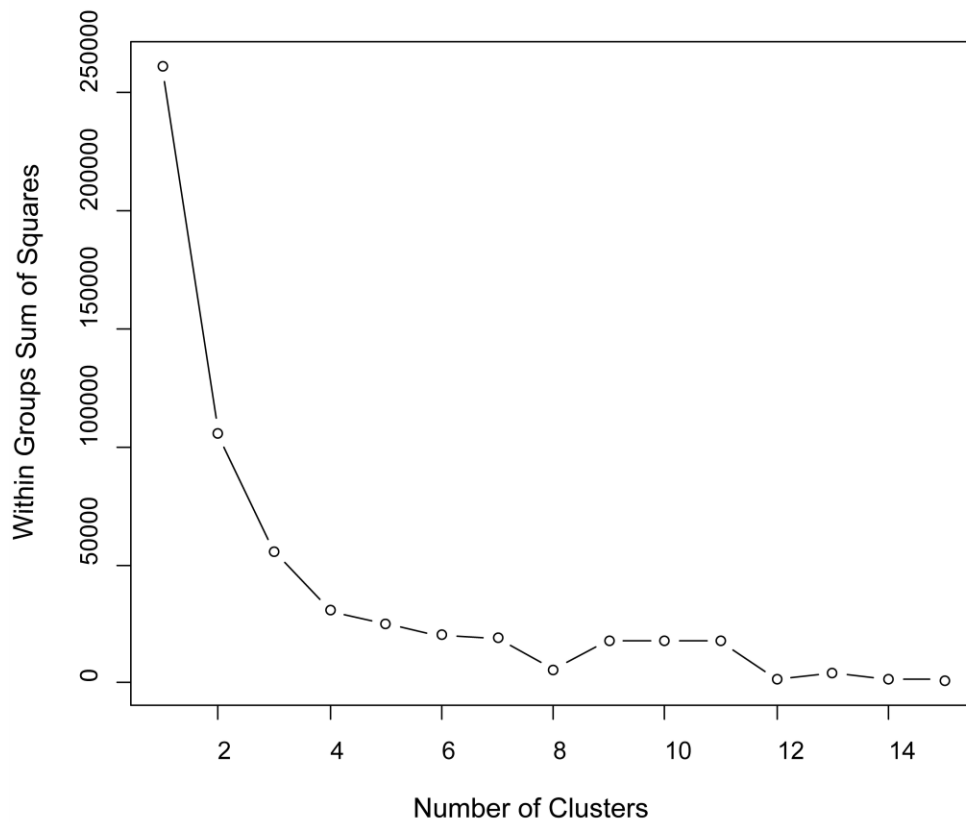
Figure 2.3. A within group sum of squares plot against number of clusters was used to determine that the trajectory data set contained three separate clusters. These clusters were then referred to as movement type 1, movement type 2, and movement type 3.
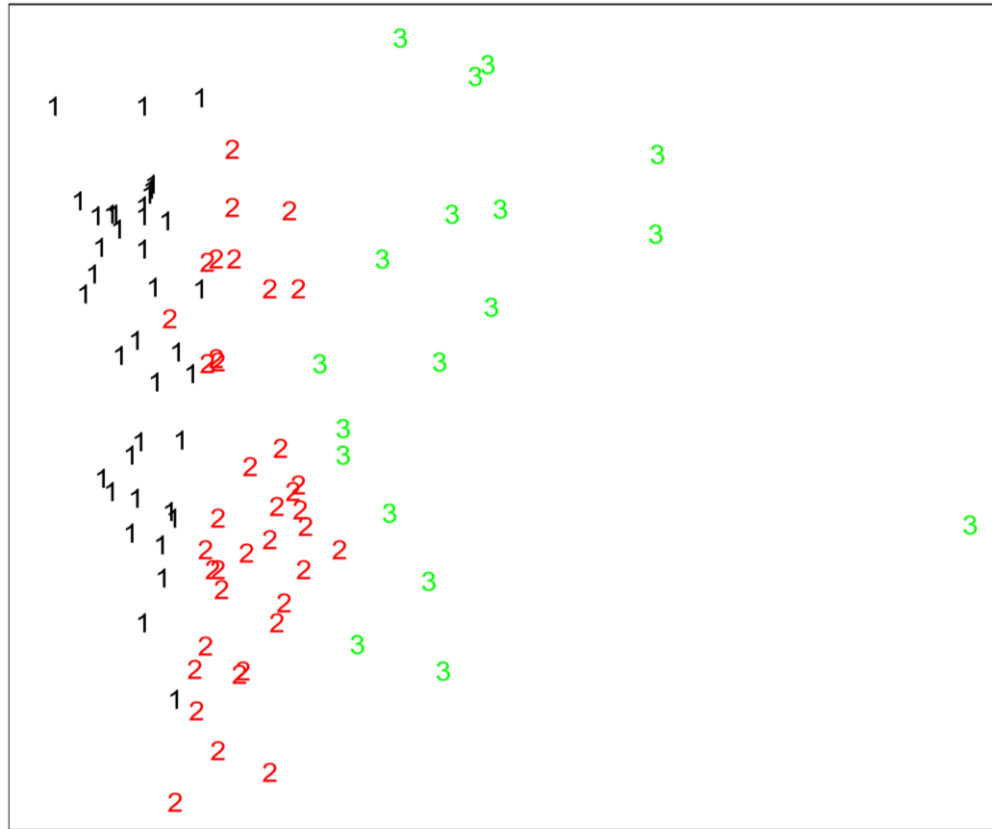
Figure 2.4. Trajectory data (n = 94) was partitioned into one of the three identified clusters (i.e., movement types 1, 2 and 3) using the k-means clustering method.

Sediment composition at study site

Sediments were characterized by grain size within the boundaries of the VPS. In 2012 a core sample was taken every 20 m parallel to the shoreline using a stainless steel corer (8 cm diameter x 11 cm height) at low tide and frozen in the lab until further analysis (Figure 2.5). For grain size analysis, samples were defrosted and the Imhoff volumetric method was employed. This involved mixing the sample with 1 L of water in a blender and pouring the mixture into a graduated Imhoff cone. Sufficient time (average 20 minutes) allowed the various components to settle. Once settled, the ratios of

sand/clay were identified, with sand settling to the bottom, followed by the clay. Ratios

were calculated for 34 samples and sediment contours were generated through inverse

distance weighted interpolations using the *Spatial Analyst* package in ArcMap (ESRI

2011).
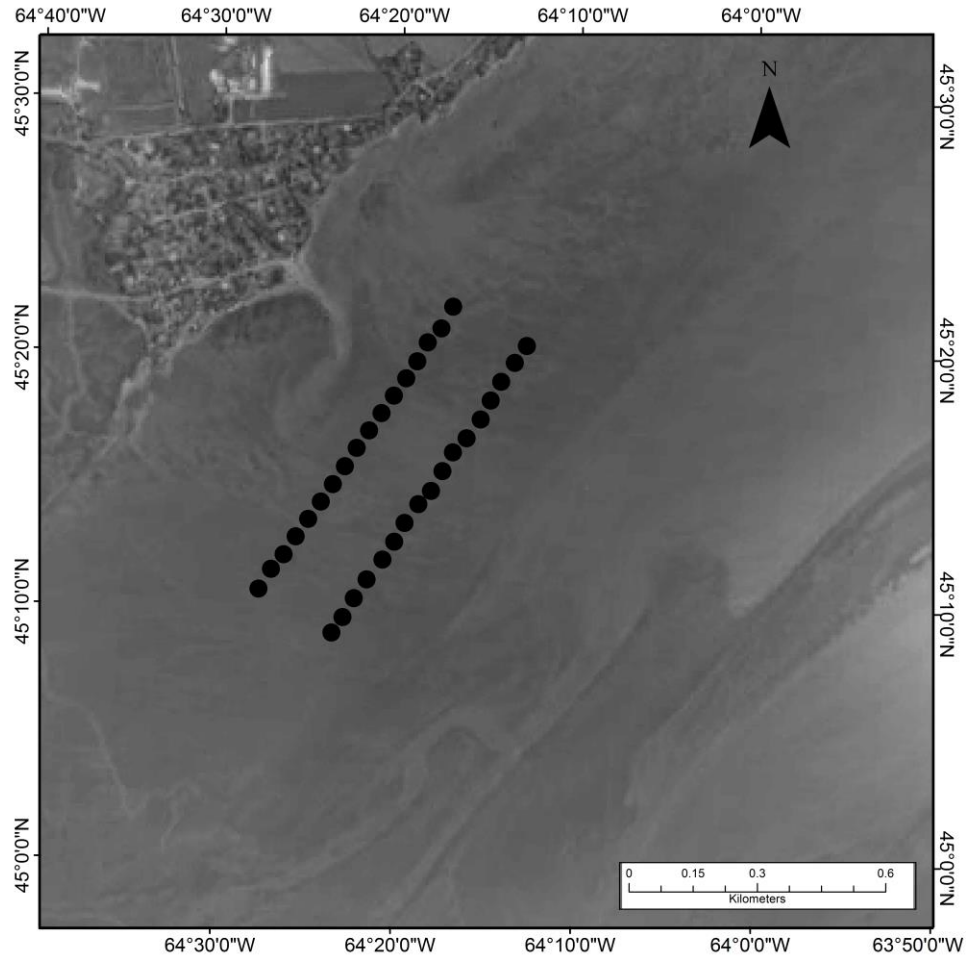
Figure 2.5. Sediment samples were collected from 34 locations within the Vemco

Positioning System array during summer 2012. Black circles indicate sampling locations.

RESULTS

Trajectories and movement types

Of the 83 sturgeon tagged, 33 were detected within the boundaries of the array between June 14th and October 6th, 2011 (Figure 2.6). After HPE and relocation filtration, 25 individuals were analyzed for fine-scale patterns. The mean fork length ± SD of all monitored sturgeon was 128.8 ± 17.5 cm (Table 2.2).

The number of analyzed trajectory bursts per tagged sturgeon ranged from 1 to 20 (Table 2.3), with 94 bursts analyzed in total. Combinations of calculated metric variables categorized each burst into one of three movement types based on those values. Mean distance travelled, mean turn angle, mean ROM and linearity were the remaining non-confounding metric variables used for further analysis (Figure 2.7).

All movement metrics were found to significantly differ between movement types with the exception of mean turn angle (Figure 2.8). Variation between most groups was identified using Tukey's HSD. Movement type 1 and 3, however, were not significantly different from each other when linearity was the tested factor. Movement type 1 was characterized by low mean distance traveled, low ROM, and a medium linearity value (Figure 2.9). Movement type 2 was characterized by medium mean travel distance, high ROM, and a high linearity value (Figure 2.9). Lastly, movement type 3 was characterized by a high mean distance of travel, high ROM, and a low linearity value (Figure 2.9).
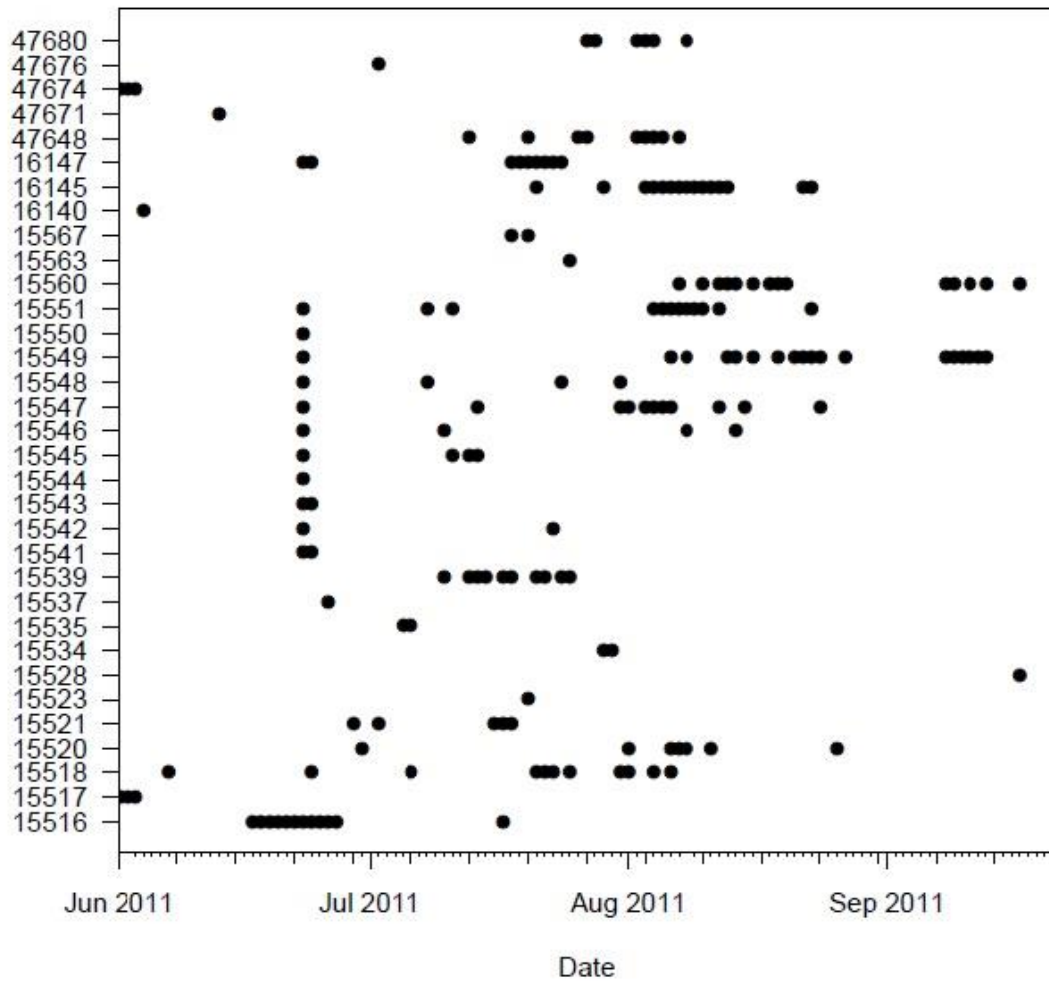
Figure 2.6. Residency plot for 33 acoustically tagged Atlantic sturgeon in the Vemco

Positioning System array at Kingsport Beach, Minas Basin, between June and October,

2011. Black circles indicate a single detection made by a tagged individual at a certain

period in time.

Table 2.2. Summary of acoustic telemetry data for Atlantic sturgeon (n = 25) tracked in a Vemco Positioning System array at Kingsport Beach, Minas Basin; FL: fork length; Wt: body wet weight.

Tag ID	FL (cm)	Wt (kg)	Date Released (mm/dd/yyyy)
16140	139	21.5*	08/17/2010
16145	124	16.5*	08/19/2010
16147	153	26.1*	08/19/2010
47648	127	17.5*	08/17/2010
47671	119	14.9*	08/19/2010
47674	124	16.5*	08/19/2010
47680	113	12.9*	09/06/2010
15516	115	11.5	06/02/2011
15518	147	22.0	06/04/2011
15520	123	16.2*	06/14/2011
15521	128	15.5	06/16/2011
15523	163	37.0	06/18/2011
15534	156	27.2*	07/08/2011
15539	144	23.1*	07/08/2011
15541	128	18.0*	07/08/2011
15542	117	14.4*	07/08/2011
15543	145	23.6*	07/08/2011
15546	112	12.5*	07/08/2011
15547	105	10.2*	07/08/2011

15548	110	12.0*	07/08/2011
15549	101	8.9*	07/08/2011
15550	110	11.9*	07/08/2011
15551	124	16.5*	07/08/2011
15560	132	19.1*	07/26/2011
15567	121	15.5*	07/26/2011

Note: * weights were estimated using the weight-length regression as follows: Wt = 0.33 FL − 24.22, where Wt is weight in kilograms and FL is fork length in centimetres.

Table 2.3. Summary of trajectory analysis for Atlantic sturgeon tracked in Vemco Positioning System at Kingsport Beach, Minas Basin. The number of analyzed bursts for each sturgeon ID is given. The mean number of calculated relocations (± Standard Deviation; SD) was determined for all bursts for a particular ID. These measurements do not take into account time spent outside of the array in between those detections.

Tag ID	No. Bursts	Mean No. Calculated Relocations ± SD	Date Begin (First Burst)	Date End (Final Burst)
16140	1	20.0	20/06/2011 5:05	20/06/2011 5:31
16145	20	30.5 ± 40.1	05/08/2011 19:35	07/09/2011 18:35
16147	4	11.0 ± 5.0	04/08/2011 5:45	08/08/2011 17:12
47648	8	22.0 ± 8.3	11/08/2011 8:56	22/08/2011 20:51
47671	1	31.0	28/06/2011 20:21	28/06/2011 21:01
47674	1	6.0	18/06/2011 3:37	18/06/2011 6:37
47680	3	27.0 ± 23.6	12/08/2011 3:37	19/08/2011 6:42
15516	2	89.0 ± 73.5	04/07/2011 16:57	06/07/2011 9:00
15518	7	15.3 ± 11.5	23/06/2011 3:40	19/08/2011 20:17
15520	5	16.6 ± 16.9	16/08/2011 16:05	26/08/2011 10:59
15521	3	33.7 ± 32.9	14/07/2011 11:53	03/08/2011 4:30
15523	2	11.0 ± 8.5	04/08/2011 14:54	04/08/2011 20:30
15534	1	9.0	14/08/2011 4:34	14/08/2011 5:01
15539	1	12.0	30/07/2011 0:49	30/07/2011 3:33
15541	3	16.3 ± 3.2	08/07/2011 22:36	09/07/2011 10:49
15542	2	28.0 ± 1.4	08/07/2011 17:26	07/08/2011 21:53
15543	2	33.0 ± 8.5	08/07/2011 17:44	09/07/2011 7:14
15546	1	27.0	23/08/2011 19:33	23/08/2011 21:28
15547	3	7.0 ± 2.7	08/07/2011 17:19	21/08/2011 16:39
15548	2	32.5 ± 21.9	08/07/2011 17:31	08/08/2011 23:01
15549	1	21.0	08/07/2011 17:56	08/07/2011 19:00
15550	1	43.0	08/07/2011 18:09	08/07/2011 19:58
15551	9	26.1 ± 43.5	08/07/2011 18:49	27/08/2011 7:32
15560	9	33.8 ± 20.7	22/08/2011 16:05	26/09/2011 16:02
15567	2	8.0 ± 2.8	03/08/2011 1:45	04/08/2011 14:33
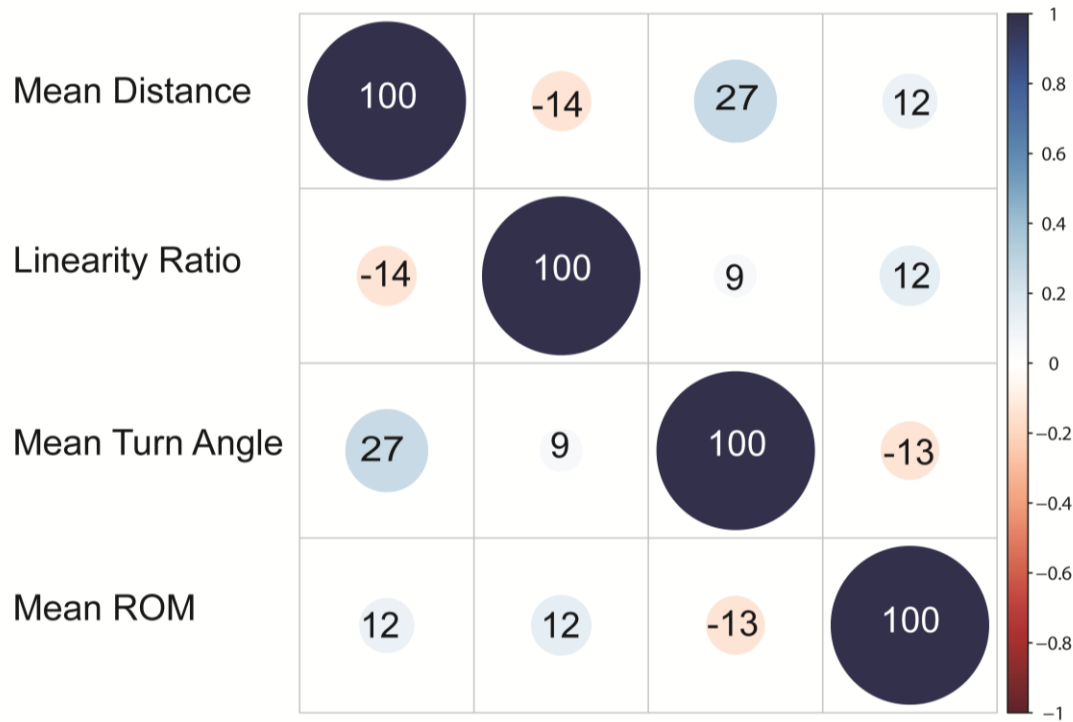
Figure 2.7. Correlation matrix of movement metrics used in trajectory analysis. Numbers given are percentages. Metrics include: Mean Dist = mean distance travelled between calculated relocations, Linearity = linearity (or straightness) of movement trajectory, Mean Turn Angle = mean turn angle of movement trajectory, and Mean ROM = mean rate of movement travelled.
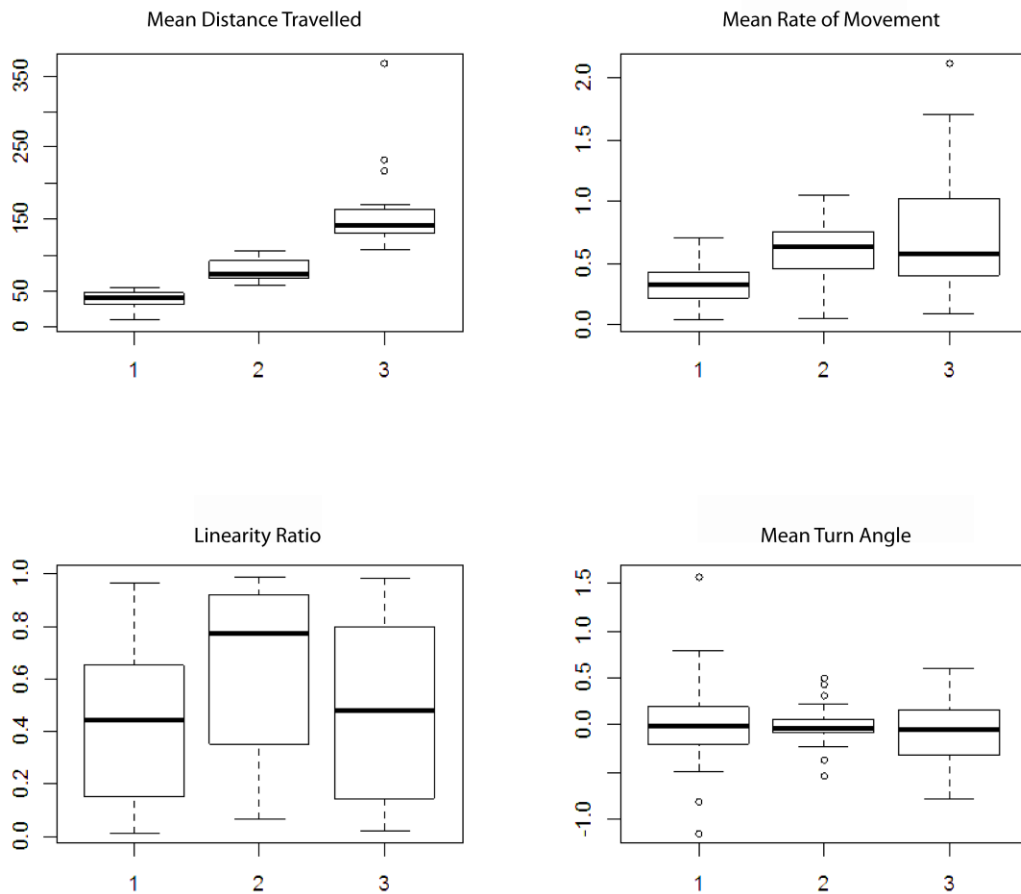
Figure 2.8. Four calculated metric variables used to distinguish movement types in Atlantic sturgeon burst trajectories. X-axis represents movement types 1, 2, and 3, respectively. Univariate analyses of variance were used to test for significance. All $P <$ 0.05, except mean turn angle. Tukey's honestly significant difference post hoc test was used for all significant categories (i.e., mean distance, mean ROM, and linearity). There was significant variation between all three movement types in each category with the exception of the linearity values of movement type 1 and movement type 3.
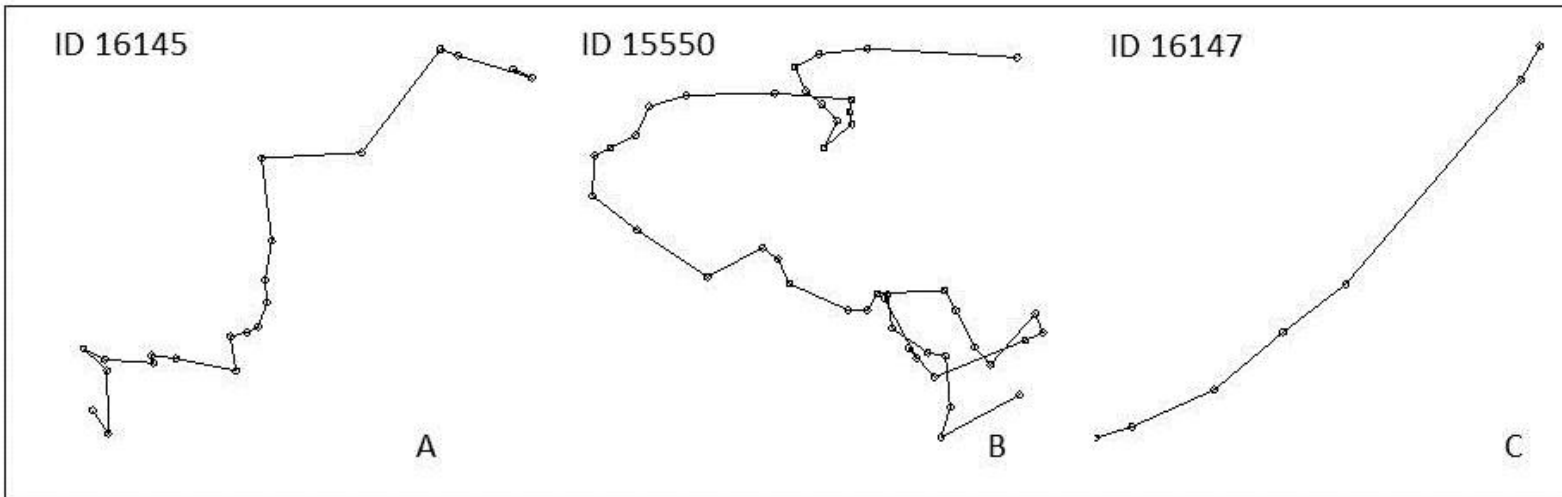
Figure 2.9. Examples of trajectories in each of three movement types. **A)** Movement type 1 trajectories were characteristically slow and winding or "S"-shaped, with short steps in between relocations. Total distance moved by sturgeon ID 16145 was 1044.29 m, with a mean distance of 52.22 m between relocations. The linearity ratio for this trajectory was 0.61, and mean ROM was 0.29 m/s; **B)** Movement type 2 trajectories were fast and tortuous. Total distance moved by sturgeon ID 15550 was 3019.19 m, with a mean distance of 71.89 m between relocations. The linearity ratio for this trajectory was 0.19, and mean ROM was 0.49 m/s; **C)** Movement type 3 trajectories were fast and linear, with large steps in between relocations. Total distance moved by sturgeon ID 16147 was 856.09 m, with a mean distance of 142.68 m between relocations. The linearity ratio for this trajectory was 0.98, and mean ROM was 0.78 m/s.

Considerable variability in the type of movement displayed by tagged individuals was demonstrated. Overall, 11/25 individuals performed three or more bursts during their monitoring period. One of the eleven displayed a single type of movement, two individuals displayed two types of movement, and eight displayed all three movement types at some point during their monitoring period indicating that most sturgeon switch from one movement type to another and do not continuously exhibit the same movement pattern. When all trajectory bursts were compared, movement types 1 and 2 were more common than the third. Overall, 40.4% of bursts were classified as movement type 1, 40.4% as movement type 2, and 19.2% as movement type 3.

Diel and tidal activity

Sturgeon were most active during dawn and dusk (Figure 2.10), but time of day was not found to be a significant predictor of movement type. All movement types occurred at varying times throughout a 24 h period (n = 94, df = 1, p = 0.13).

Sturgeon were detected more often during a flood, rather than an ebb tide, however, the type of movement (i.e. Types 1, 2, and 3) did not differ significantly between the flood and the ebb tides (Chi^2 = 0.97, df = 2, p = 0.62). Movement types did not differ significantly at various water levels (i.e., high, low, mid/slack; Chi^2 = 6.07, df = 4, p = 0.19).

Sediment composition at study site

The mean (± SD) clay to sand ratio at Kingsport Beach (Figure 2.1) is 0.3 ± 0.2 (Figure 2.11 and 2.12), which means much of the area is composed of sandy/silt sediments with small patches of sand, silt, and clay dispersed throughout.
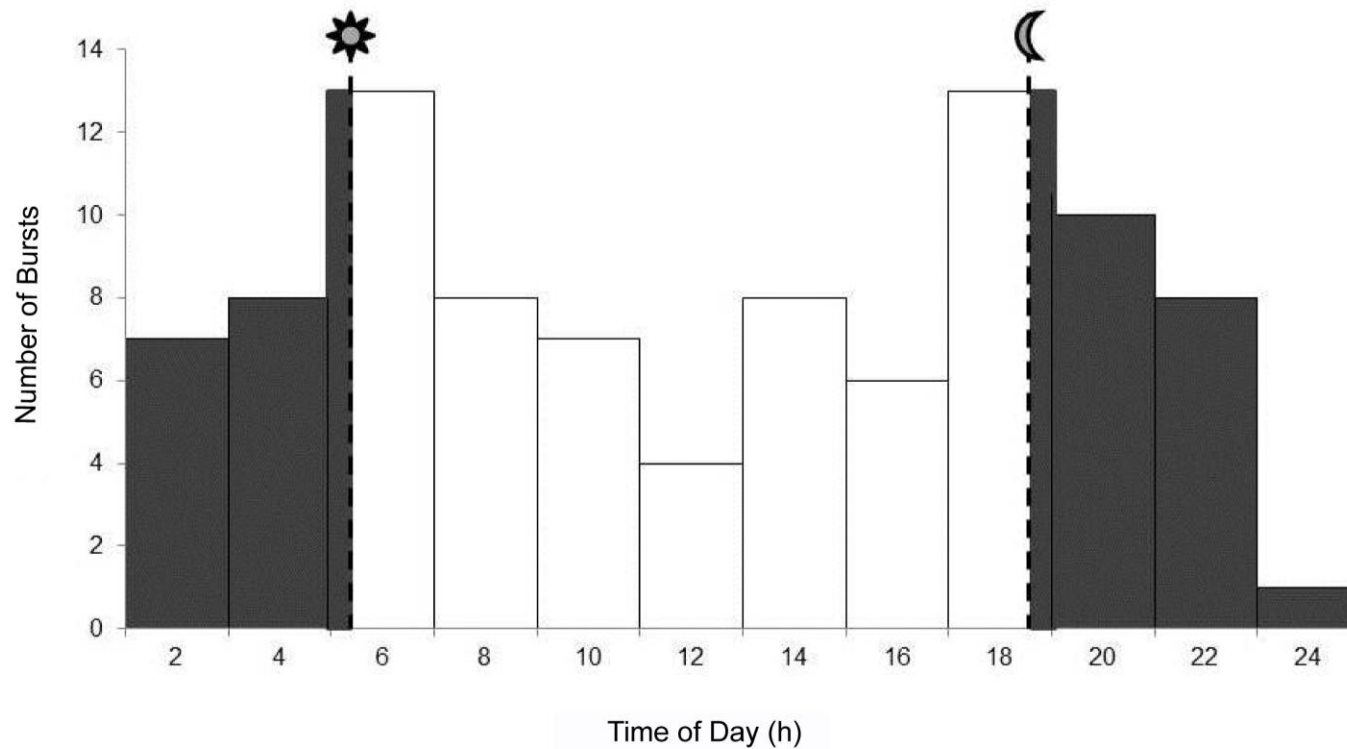
Figure 2.10. Frequency of occurrence for sturgeon bursts during time of day showing increased crepuscular activity by tagged Atlantic sturgeon. Shaded areas are indicative of nighttime. Dashed lined represent the average sunrise and sunset times for Minas Basin from June to October, 2011.
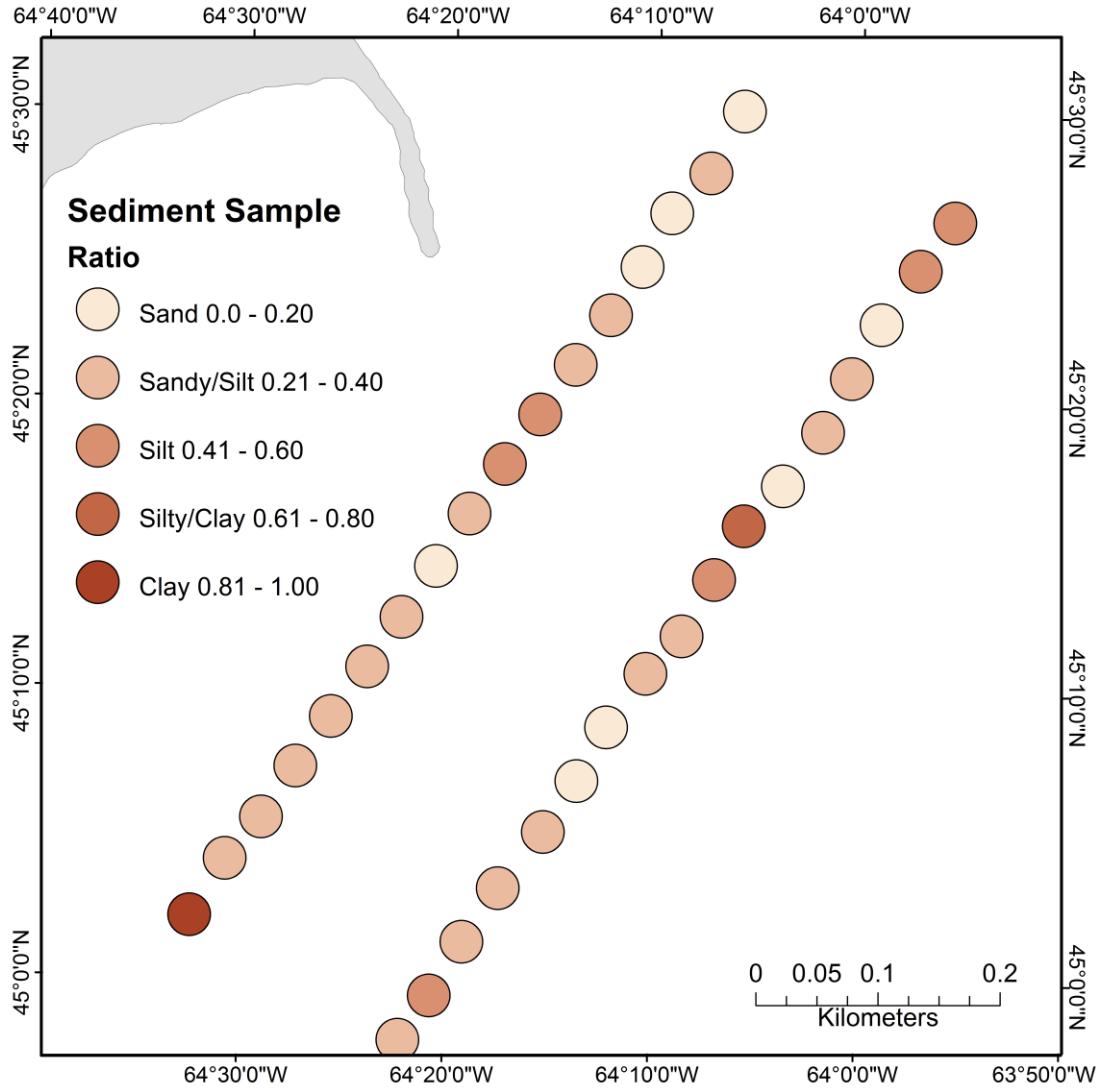
Figure 2.11. Sediment ratios were identified for samples collected from Kingsport Beach intertidal zone within the Vemco Positioning System array.
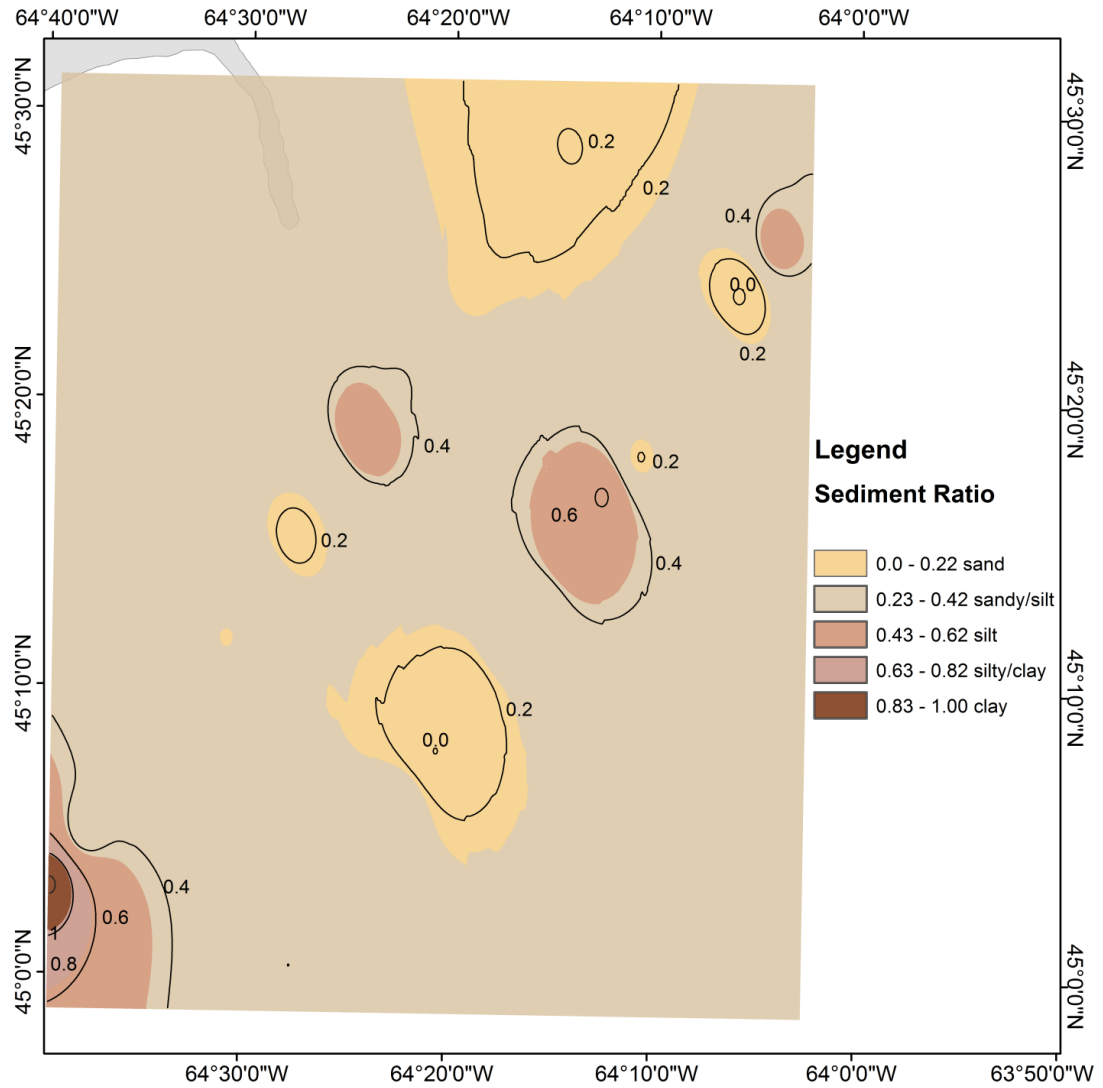
Figure 2.12. Sediment ratio data was interpolated to create sediment ratio contours as a descriptor of bottom type within the Vemco Positioning System array.

DISCUSSION

Using calculated relocations from an intertidal VPS I successfully identified three different movement patterns exhibited by adult Atlantic sturgeon. These results may provide the first step in a more detailed understanding of behavioural drivers underlying movement data. The main differences between identified behaviours were swim speed (ROM), distance between relocations, and linearity of the trajectory. These movement metrics revealed fine-scale behavioural shifts not previously described for adult Atlantic sturgeon. Directional and non-directional movements have been described for green sturgeon (*Acipenser medirostris* Ayres, 1854) based on swim speed and depth metrics (Kelly et al. 2007). Non-directional behaviour consisted of slow and erratic movements on or near the substrate, whereas directional behaviour was faster, more linear and higher in the water column where occasionally the fish actively moved to cover long distances (Kelly et al. 2007). Although motivation behind exhibited behaviour is difficult to confirm without visualization, studying the fine-scale movements in relation to other factors such as environment and/or prey availability, provides an important understanding of an animal's life-history.

Non-directional behaviour displayed by green sturgeon was presumably associated with foraging in areas of high prey abundance (Kelly et al. 2007). Foraging behaviour has been experimentally observed for a number of sturgeon species. To examine olfactory cues in relation to various behaviours Kasumyan (1999) put adult green, Russian (*Acipenser guelenstaedtii* Linnaeus, 1758), Siberian (*A. baerii* Brandt, 1869), stellate (*A. stellatus* Pallas, 1771), and beluga (*Huso huso* Linnaeus, 1758) sturgeon in holding tanks and observed swimming behaviour in response to prey odours

which were placed randomly within the tank. Kasumyan (1999) recognized a crowding

by sturgeon to areas containing maximum concentrations of food odour and once the area

was located, sturgeon began to move in winding or "S"- shaped trajectories trailing

barbells on the substratum and often attacking the bottom in an attempt to ingest food. In

our study, movement type 1 appears to be indicative of this same feeding behaviour as

many of the trajectories in this category were winding with slow movements and short

time steps. A change in movement, particularly lowering of swim speed and decrease in

turn rate may be an approach to intensify the search within a prey patch. If sturgeon

located a reliable prey source, then the short steps between relocations may indicate

feeding within that patch.

A change from one movement type to another may be driven by a number of

factors including increased competition for resources, changing prey availability, or the

risk of predation (Heupel et al. 2012). In addition to these factors, mobile species in the

Minas Basin have to accommodate the extreme semi-diurnal tidal fluctuations which

limit intertidal foraging time and increase the demand for optimal foraging practice. In

our study, movement type 2 trajectories were erratic and tortuous and resembled a

searching pattern. Because of the tortuous nature of these movements, a large area of the

intertidal zone was often covered during a single analyzed trajectory. Searching

behaviour by sturgeon was also experimentally examined by Kasumyan (1999) who

observed an immediate disruption of regular swimming activity upon delivery of the

odour solution, followed by increased swimming speed, and occasional bursts along the

path of movement. As sturgeon passed through the odour zone occasionally they would

reverse course and rapidly return along a circular trajectory "searching" for the odour

(Kasumyan 1999). The most notable change in behaviour was swim speed, which rapidly increased as the odour spread, as well as sudden changes in direction of movement (i.e. increased tortuosity; Kasumyan 1999). Increased sinuosity is common in foraging animals and most foraging animals decrease swimming speed when patches of high food abundance are encountered (Coughlin et al. 1992). In our case, movement type 2 may be representative of a searching behaviour whereas movement type 1 is a behaviour adopted once a suitable prey patch is identified. Since most individuals performed all three movement types at some point during the study, it is not unreasonable to suggest that the change from one movement type to another may be driven by foraging activity in the intertidal zone.

Atlantic sturgeon also made rapid, straight-line travel movements (i.e. Movement type 3), however, these were not as frequent as the other two types of movement and generally occurred outside of the intertidal zone. Movement type 3 occurred in the deeper water off the intertidal zone at the Cornwallis River estuary mouth where large influxes of fresh water enter the Minas Basin from three rivers; the Cornwallis, Canard, and Habitant. Generally due to strong currents, high turbidity, low average salinity and variable temperatures found within the estuary, there are markedly fewer organisms residing there in contrast to the salt marshes and tidal flats surrounding it (Daborn et al. 2004). Rapid, straight-line travel can represent an extensive search mode in areas of poorer food quality as animals try to minimize the time spent between patches and reduce the chance of repeat visits to the same patch (Zollner and Lima 1999). Thus, rapid, straight-line travel may represent transitory movement through this area indicative of movement between patches of food. Unlike movement types 1 and 2, type 3 did not occur

in the intertidal feeding zone, which further supports the idea that movement types 1 and 2 are behaviours primarily associated with searching or foraging practice.

McLean et al. 2013 collected and analyzed Atlantic sturgeon stomach samples concurrently during the deployment of acoustic tags of this study. Their results indicated a high proportion of prey items consumed are benthic polychaete worms, primarily *Clymanella* spp. and *Spiophanes bombyx*, both present on the Minas Basin mudflats. Atlantic sturgeon diet analyses in other oceanic and estuarine systems have also reported a dietary preference for benthic invertebrates (Johnson et al. 1997; Haley 1999; Savoy 2007; Guilbard et al. 2007). The polychaete species comprising over 99% of the Atlantic sturgeon diet in Minas Basin are more abundant in low and mid-intertidal regions (Glenys Gibson, *personal communication*) and inhabit substrates with larger grain sizes (Hicklin and Smith 1984). Bottom-type within the VPS study area was primarily sandy/silt with patches of mud, silt and sand. This patchiness in sediment type may reflect on the benthic invertebrate distribution and might explain some of the observed behaviours by tagged Atlantic sturgeon searching for suitable bottom type and prey patches.

Sturgeon are not visual predators and rely on their well-developed chemosensory and taste systems to locate prey (Kasumyan 1999; Miller 2004). Although time of day was not a significant predictor of the movement type a tagged individual displayed, an increase in overall activity was recognized at dawn and dusk that may represent an important temporal activity pattern not previously documented for adult Atlantic sturgeon. Two hypotheses have been postulated regarding sturgeon foraging. The first is that nocturnal foraging occurs (Haynes and Gray 1981) and the second is that foraging is continuous throughout the day (McKinley and Power 1992).

Nocturnal behaviour has been described for other sturgeon species, including the white sturgeon, which increased swimming speeds at night and occupied shallower waters than during the day (Parsley et al. 2008). The increased rate of movement does not necessarily imply increased foraging behaviour, but may suggest that sturgeon were making diel migrations to exploit prey that is more prevalent in shallower water at night or to follow mobile prey (Parsley et al. 2008). The white sturgeon diet consists of invertebrates as well as some species of fish (McCabe et al. 1993) so following migratory mobile prey that are more active at night may explain the nocturnal patterns observed. Atlantic sturgeon diet rarely consists of other fish species, however the occasional sand lance (*Ammodytes* spp.) has been noted (Dadswell 2006). Sand lances are present in the Minas Basin, but there is no record of the summer aggregation of Atlantic sturgeon in Minas Basin feeding on them so the tracking of mobile prey is not a likely explanation for the diel patterns observed during this study. Most of the Minas Basin aggregation of Atlantic sturgeon feed solely on tube-dwelling polychaetes (McLean et al. 2013) which are primarily negatively phototactic but often rely on light cues at dawn and dusk to synchronize reproductive activities (Rupert et al. 2004). Oligochaetes have also been identified as being positively phototactic to dim light levels such as would occur during dawn and dusk. Therefore I hypothesize that the increased crepuscular activity displayed by Atlantic sturgeon is partially related to prey availability.

Fishes in Minas Basin have been found to follow the movement of the tide onto the intertidal zone for high tide and off again for low tide (Rulifson et al. 2008). In this study Atlantic sturgeon entered the study area on a flood tide more often than on an ebb tide, suggesting that they were moving with the flooding tide, likely to increase the

amount of foraging time on the mudflats. While tidal stage and water-level were not significant factors in observed movement types, tidal stage is likely still critical to the movements of individuals overall (i.e., foraging habitat accessibility). This pattern has also been observed in a number of shark species. The leopard shark (*Tirakis semifasciata* Girard, 1855) significantly moved towards the inner bay with the incoming tidal currents presumably to exploit food resources made available by the rising tides (Ackerman et al. 2000). Similarly, in another California estuary, female leopard shark distribution and movements were strongly influenced by the tides and in some regions of the estuary the sharks would move with the tide in order to maximize the area over which they could forage (Carlisle and Starr 2010). Like foraging sturgeon, leopard sharks display a high degree of plasticity in diet and are often recorded foraging on different prey items depending on what is locally available (Carlisle and Starr 2010). By moving with the tide, individuals are able to gain access to the different prey items that are abundant in various areas of the estuary therefore increasing their likelihood of discovering a suitable prey patch.

The quantification of movement paths can provide a technique to improve our understanding of the foraging strategies of marine predators in a system where direct observations of feeding behaviour are rare (Bailey and Thompson 2006). The use of movement metrics to quantify movement patterns of tagged Atlantic sturgeon successfully revealed three behaviours expressed by individuals. Identifying fine-scale movement patterns of animals can provide insight into understanding the drivers behind the movements made. For Atlantic sturgeon, much of this incentive is likely foraging strategy as they exploit the tidal flats at high tide. Since successful food acquisition is

crucial to an animal's growth, reproductive viability, survival and fitness, identifying important foraging areas through observing foraging behaviour allows for the characterization of critical habitat that plays a central role in developing proper management strategies for protecting species of concern.

This technique could be applied to a number of acoustically tagged aquatic species for comparisons of how individuals move and the identification of patterns in the movement both spatially and temporally. Overall, this method could help us to better understand population structure and resource use of aquatic animals and may provide information on optimal foraging strategies pertinent to an animal's fitness and survival.

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GENERAL CONCLUSION AND RECOMMENDATIONS
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In this dissertation I described the feeding behaviour and movement of Atlantic sturgeon in a macro-tidal estuary, and attempted to link these behaviours to their physical and biotic drivers. The studies were performed in the Minas Basin, Nova Scotia. Large numbers of Atlantic sturgeon from rivers as far south as Virginia and as far north as New Brunswick, all under various conservation listings, seasonally aggregate in the Minas Basin (Wirgin et al. 2012). The Minas Basin is a dynamic ecosystem primarily because of its large semi-diurnal tides which leave a large portion of the Basin inaccessible to foraging groundfish at low tide.

In my first research chapter I described the diet of subadult/adult Atlantic sturgeon. Atlantic sturgeon were primarily feeding on sand tube dwelling polychaete species commonly found in the intertidal mudflats. Primary components of the diet were multiple species of bamboo worm, *Clymanella* spp., and *Spiophanes bombyx*. These results corroborated with the findings of other Atlantic sturgeon diet studies which suggested that a high proportion of the adult diet was comprised of soft-bodied invertebrates.

An examination of gut fullness did not reveal a difference in diet composition between two study sites in Minas Basin, nor was a difference identified in diet composition between various sizes of Atlantic sturgeon. Ontogenetic shifts in diet have been described for Atlantic sturgeon, however, most of this work compares young juveniles with adults. Young juvenile Atlantic sturgeon are not common in the Minas Basin (Wehrell et al. 2008).

In my second research chapter I quantified the movement patterns of acoustically tagged Atlantic sturgeon within the intertidal zone of Kingsport Beach, Minas Basin. Through the analysis of fine-scale spatial data on Atlantic sturgeon movement, three distinct patterns of behaviour were identified. Two of the behaviours were indicative of foraging and searching, and occurred over sand/silt sediment in the intertidal zone. These sediments are known to support polychaetes *Clymanella* spp. and *Spiophanes bombyx* corroborating the findings of chapter one and strongly linking feeding and sand/silt habitat structure. The third movement type identified was indicative of transitory behaviour and suggests there were times where Atlantic sturgeon were moving past the general study site without actually foraging on the mudflats. These movements were made outside of the study area and within the outflowing of two rivers that drain into the southern bight near Kingsport.

Each movement type was compared to environmental factors such as tidal fluctuations and diel cycle. Perhaps not surprisingly all movement types were equally as likely to occur during all tidal stages. In environments where the tidal variation is not as extreme, a more distinct foraging pattern may be discernible. Other sturgeon species have been identified as nocturnal feeders, however, in Minas Basin Atlantic sturgeon appear to be taking advantage of the tides and, regardless of time of day, are following the tide in at high tide and back out at low tide. Although there was no difference in movement type and time of day an overall increase in activity occurred during dawn and dusk. This increased crepuscular activity is a temporal pattern not previously described for adult Atlantic sturgeon.

Sturgeons are one of the most primitive extant families of bony fishes. Cultural ties to these fish pre-date European settlers and although they are infrequently marketed as a food fish, there are still valuable markets for their roe for luxury caviar. Currently, Atlantic sturgeon populations are protected in various ways in both Canada and the US. Life-history characteristics such as slow growth, intermittent spawning, and late maturity have further impeded the recovery of certain depleted stocks.

Trans-boundary fish, such as Atlantic sturgeon, complicate protection and management strategies implemented by various jurisdictions. Information on Atlantic sturgeon movement and identification of critical feeding habitat will help managers determine areas in marine, estuarine, and freshwater systems that are important to the health, viability and productivity of sturgeon populations. The development of a holistic approach to the management and conservation of Atlantic sturgeon will require much more information on the basic biology of the species. An assessment of overwintering sites and important oceanic migration pathways will help us to further understand the importance of the Minas Basin to the summer aggregation of sturgeon. This baseline information will also serve as comparative data for any future impact assessment studies.

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List of Appendices

Appendix I. – Numerical values for prey taxa abundance, occurrence, and wet weight collected from Atlantic sturgeon stomachs.

Appendix II. - Detailed trajectory profiles of acoustically tagged Atlantic sturgeon.

Appendix I. Relative occurrence (%O), mean abundance (%N), and mean wet weight (%W) of taxa collected in the stomach contents

of Atlantic sturgeon (n = 20) during the summer of 2011 in Minas Basin, Bay of Fundy.

No.	Class	Family	Occurrence	%O	Total number	%N	Wet Weight	%W	IRI	%IRI
1	Polychaeta	Maldanidae	18	90	2011	37.18565089	52286	43.54057	7265.36	52.51079
2	Polychaeta	Spionidae	12	60	3013	55.7137574	48208	40.14466	5751.505	41.56932
3	Polychaeta	Phyllodocidae	11	55	148	2.736686391	2960	2.464906	286.0876	2.067714
4	Polychaeta	Nephtyidae	10	50	83	1.534763314	5395	4.492625	301.3694	2.178164
5	Polychaeta	Neireididae	6	30	24	0.443786982	3497	2.912087	100.6762	0.727643
6	Polychaeta	Glyceridae	4	20	29	0.536242604	4445.7	3.702106	84.76697	0.612658
7	Polychaeta	Syllidae	4	20	18	0.332840237	240	0.199857	10.65395	0.077002
8	Malacostraca	Corophiidae	3	15	5	0.092455621	25	0.020818	1.699111	0.01228
9	Crustacea	Aoridae	2	10	2	0.036982249	20	0.016655	0.53637	0.003877
10	Sipunculadea	Sipunculidae	2	10	44	0.813609467	1320	1.099215	19.12824	0.13825
11	Polychaeta	Capitellidae	2	10	11	0.203402367	660	0.549607	7.530099	0.054424
12	Malacostraca	Mysidae	2	10	3	0.055473373	15	0.012491	0.679645	0.004912
13	Polychaeta	Goniadidae	1	5	2	0.036982249	16	0.013324	0.25153	0.001818
14	Gastropoda	Pyramidellidae	1	5	1	0.018491124	989	0.823578	4.210348	0.030431
15	Polychaeta	Scalibregmatidae	1	5	1	0.018491124	5	0.004164	0.113274	0.000819
16	Maxillopoda	Oithonidae	1	5	1	0.018491124	5	0.004164	0.113274	0.000819
17	Crustacea	Idoteidae	1	5	1	0.018491124	5	0.004164	0.113274	0.000819
18	Crustacea	Diastyidae	1	5	1	0.018491124	5	0.004164	0.113274	0.000819
19	Crustacea	Crangonidae	1	5	1	0.018491124	5	0.004164	0.113274	0.000819
20	Polychaeta	Arenicolidae	1	5	3	0.055473373	5	0.004164	0.298185	0.002155
21	Polychaeta	Tomtopteridae	1	5	4	0.073964497	5	0.004164	0.390641	0.002823
22	Malacostraca	Gammaridae	1	5	1	0.018491124	5	0.004164	0.113274	0.000819
23	Polychaeta	Paraonidae	1	5	1	0.018491124	5	0.004164	0.113274	0.000819
Total					5408	100	120085.7	100	13835.94	100

Appendix II. Detailed trajectory profiles of acoustically tagged Atlantic sturgeon for each burst used in the analysis of this study. Included in each profile are the individual acoustic tag ID number, the burst number pertaining to each ID, and the classified movement type for that burst based on analysis.

| 15516 Burst 1 Movement type: 1 | 15516 Burst 2 Movement type: 1 |
| 15518 Burst 1 Movement type: 2 | 15518 Burst 2 Movement type: 1 |