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# Atlantic sturgeon *Acipenser oxyrinchus* Mitchill, 1815 seasonal marine depth and temperature occupancy and movement in the Bay of Fundy

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**Summary**

Pop-up satellite archival tags were used to collect fisheries-independent data that characterized the seasonal habitat occupancy and movement of Atlantic sturgeon *Acipenser oxyrinchus* Mitchill, 1815 in the Bay of Fundy (BoF). Atlantic sturgeon from Canadian and United States stocks aggregate annually for feeding in Minas Basin, inner BoF (45.28N, 64.18W), during May to September but depart to other locations from October to April. Sixteen PSAT tags were applied to sturgeon ranging from 152 to 203 cm total length captured and released in Minas Basin during May to August. Ten of the tags were reported after 1 year at large and provided pop-off locations. Seven were recovered with archived data, or provided transmitted data sets, which were analyzed for depth and temperature occupancy from June 2011 to August 2013. During June to August while in the Minas Basin the sturgeon spent >90% of time at depths <10 m and temperatures of 16–22°C. Departure from Minas Basin through the Minas Passage was in September and October, when depth occupancy varied from <10 to 120 m. From November to April sturgeon were in the outer BoF, where mean depth occupancies ranged from 40 to 100 m at mean temperatures of 3–14°C. Deepest mean depth occupancy of 60 to 90 m was recorded during December 2011 and 2012, and coldest mean temperature occupancy of 0–4°C in March 2011 and 2012. During April and May mean depth and temperature occupancy ranges shallowed from 40 to <10 m and increased from 4 to 15°C, respectively. Tag pop-off locations indicated that sturgeon spent the winter season in the outer BoF but by June had either migrated back to the Minas Basin or off the mouth of the Saint John River, a known spawning location.

## 1 | INTRODUCTION

A major component of the life history of many anadromous, estuarine and coastal marine fishes is that they occupy marine habitats and undertake migrations to feed, reproduce and maintain themselves in a physiologically acceptable environment (Leggett & Whitney, 1972; Quinn & Leggett, 1987). Habitat occupancy and movement is also influenced by species, age, sex and maturity (Dell'apa, Cudney-Burch, Kimmel, & Rulifson, 2014; Erickson et al., 2011; Smith & Rulifson, 2015). In the marine environment of the Bay of Fundy (BoF) fishes tend to move inshore to shallow habitats during summer, and offshore to deeper and seasonally warmer habitats during winter (Campana et al., 2008; Dadswell, Melvin, Williams, & Themelis, 1987; MacDonald, Dadswell, Appy, Melvin, & Methven, 1984; McCracken, 1963).

The Atlantic sturgeon *Acipenser oxyrinchus* Mitchill, 1815 is a large anadromous benthic-feeding fish that occurs along the east coasts of North and South America from French Giana to Labrador and formerly northern Europe (Dadswell, 2006). They spawn in freshwater habitat

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during summer, or autumn (Balazik, Garman, Van Enennam, Mohler, & Woods, 2012; Van Eenennaam & Doroshov, 1998), remain in estuaries until about 5–10 years of age and 100 cm fork length (FL), and then migrate to sea (Dadswell, 2006). Depending on their sex and the latitude of their natal river, Atlantic sturgeon mature at different ages and sizes. Male *A. oxyrinchus* spawning in Canadian rivers typically reach sexual maturity at 16–24 years and at a size of approximately 150 cm FL; females mature at ages 27–28 and at a size of 180–200 cm FL (Dadswell, 2006; Stewart et al., 2015). Juvenile and adult Atlantic sturgeon spend most of their non-reproductive periods feeding in estuaries or on the coastal shelf, but specific habitat characteristics and behaviours in marine environments are not well understood, especially for individuals occupying the northern portion of their range. The limited information available for marine coastal environments is from fisheries data (ASMFC, 2007; ASSRT, 2007; Stein, Friedland, & Sutherland, 2004; Vladykov, 1957), acoustic tracking studies (Fox, Hightower, & Parauka, 2002; Hatin, Fortin, & Caron, 2002; Lindley et al., 2008; McLean, Simpfendorfer, Huepel, Dadswell, & Stokesbury, 2014; McLeave, Fried, & Towt, 1977), and pop-up satellite archival tags (PSATs; Edwards, Parauka, & Sulak, 2007; Erickson et al., 2011).

Fishery catch records provide some information on Atlantic sturgeon marine distribution but are from a small proportion of potential habitats and subject to gear-selectivity bias (ASSRT, 2007). Dovel and Berggen (1983) reported that Atlantic sturgeon tagged with external tags in the Hudson River, NY, were recaptured to the south along the Atlantic coast to Chesapeake Bay. Recoveries in Chesapeake Bay were in coastal fisheries trap nets and predominately during winter months. The Atlantic States Marine Fishery Commission (2007) reported that sink gillnet bycatch occurred mostly in <40 m of water, and otter trawl fisheries reported bycatch centered around depths of 10–30 m. There is some evidence for latitudinal depth preferences in Atlantic sturgeon, since bycatch is greater at greater depths in the Gulf of Maine relative to bycatch in the Mid-Atlantic Bight (Stein et al., 2004). The highest incidence of Atlantic sturgeon bycatch occurred during April and May in northeastern fisheries in the United States (ASMFC, 2007). Bycatch events were typically concentrated in estuaries and over sandy substrate (McLean, Dadswell, & Stokesbury, 2013; Stein et al., 2004).

Acoustic telemetry studies indicated that sturgeons have three typical movement patterns in marine environments during the spring, summer and autumn. Their nearshore behaviour can be: (i) Oriented; (ii) Exploratory; or (iii) Wandering (Edwards et al., 2007; McLean et al., 2014; McLeave et al., 1977), and offshore behaviour may include levy search patterns (Sulak & Clugston, 1999). Acoustic tagging has demonstrated that juvenile and adult Atlantic sturgeon in the St. Lawrence River typically move into coastal marine habitats during winter months (Hatin et al., 2002), and on the west coast of Florida that Gulf sturgeon (*Acipenser oxyrinchus* desotoi) overwinter in shallow, marine coastal waters (~10 m; Edwards et al., 2007; Ross et al., 2009; Sulak & Clugston, 1999).

PSATs have been used by researchers to provide fishery-independent data for many large, highly migratory marine fish species, including tuna, sharks and Atlantic sturgeon (Block et al., 2005; Campana, Joyce, & Fowler, 2010; Edwards et al., 2007; Erickson et al., 2011; Stokesbury, Harvey-Clark, Gallant, Block, & Myers, 2005; Stokesbury, Neilson, Susko, & Cooke, 2011; Stokesbury, Teo, Seitz, O'Dor, & Block, 2004). PSAT studies found that Gulf and Atlantic sturgeon occupied near shore, marine environments in depths as shallow as 6 m during summer months (Edwards et al., 2007; Erickson et al., 2011), and off west Florida that individuals migrated along the coast up to 180 km, aggregating in overwintering areas outside of their natal spawning estuary (Edwards et al., 2007). Erickson et al. (2011) concluded that mean depths for Atlantic sturgeon were shallowest during summer months and deepest during late autumn and early winter months, demonstrating an Atlantic sturgeon coastal migration route extending from the South Atlantic Bight to Mid-Atlantic Bight using light-based geolocation data from 15 individuals. One PSAT-tagged female Atlantic sturgeon (2.24 m TL) tagged in the Hudson River on 30 July 2007 migrated over 1,000 km northeast to Minas Basin, BoF approx. 1 year later (Erickson et al., 2011). Coastal marine tracking of green sturgeon *Acipenser medirostris* Ayres, 1854 with PSATs suggest that a 1,000 km migration could take as little as 20 days (Lindley et al., 2008).

During summer a large feeding aggregation of juvenile and adult Atlantic sturgeon takes place in Minas Basin, a large cul-de-sac embayment of the inner BoF (Dadswell, 2006; McLean et al., 2013; Stokesbury, Stokesbury, Balazik, & Dadswell, 2014). The aggregation consists mainly (94%–98%) of migrants from the Saint John River, NB and Kennebec River, ME (Wirgin et al., 2012). Minas Basin is a shallow, mega-tidal, summer warm embayment (Bousfield & Leim, 1959) where sturgeon feed (McLean et al., 2013) over the extensive intertidal zone (1–5 km wide) during high tide (McLean et al., 2014). In winter, however, the inner BoF is covered by up to 5 m thick drifting ice pans and with a water temperature that declines to −1.5°C (Gordon & Desplanque, 1983). Virtually all fishes depart the inner BoF during winter (Dadswell et al., 1984).

Since Atlantic sturgeon are listed as endangered or threatened along the Atlantic coast of North America (COSEWIC, 2011; NOAA, 2012), ocean resource managers need to know where and when *Acipenser oxyrinchus* spend their marine phase in order to protect them against anthropogenic threats such as tidal and hydroelectric turbine developments (Dadswell & Rulifson, 1994; Stokesbury, Broome, Redden, & McLean, 2012), offshore drilling projects (Lindley et al., 2008) and potential fisheries bycatch (ASMFC, 2007; ASSRT, 2007; Beardsall et al., 2013; Davis, 2002).

Atlantic sturgeon are known to occupy shallow depths while feeding in Minas Basin during summer (McLean et al., 2014), but the bottom temperature ranges in winter are beyond the physiologically acceptable limits of most temperate fishes; we propose that they would exit the basin in autumn and overwinter in a marine environment where the temperature is less extreme. The inner BoF is mostly shallow and temperatures are extremely low (reaching −1.5°C) in winter (Sanderson, Redden, & Broome, 2012). We propose that the sturgeon would have to move to the outer BoF, the Gulf of Maine or onto the Scotian Shelf, where there are known overwintering sites for other fishes such as winter flounder *Pseudopleuronectes americanus* (Walbaum, 1792), American shad *Alosa sapidissima* (Wilson, 1811) and spiny dogfish *Squalus acanthias* L., 1758. These species are also abundant in Minas Basin during summer (Campana et al., 2008; Dadswell et al., 1987; McCracken, 1963). Most of the Gulf of Maine and the Scotian Shelf overwintering habitats occur at depths >40 m. To obtain evidence for winter residency habitats and movement, we tagged Atlantic sturgeon with temperature, depth and light measuring PSATs during summer while they were in Minas Basin which did not require the chance recapture of the fish.

## 2 | MATERIALS AND METHODS

### 2.1 | Study environment

The Bay of Fundy is a 300 km long, 13,500 $km^2$ embayment of the Gulf of Maine (Fig. 1). The bay is 80 km wide at its outer end and narrows to 50 km at its inner end where it divides into Minas Basin and Chignecto Bay. The outer bay has a tidal range of 5–8 m and maximum depths of 100–200 m. The tide is semi-diurnal and 170 billion $m^3$ of water is exchanged during each tide phase (Greenburg, 1984). The outer BoF is a highly productive marine environment due to upwelling that is caused by the constant and intense tidal mixing (Garrett & Loucks, 1976). Bottom temperatures in the outer BoF range from 10.3°C in summer to 1.7°C in winter, with an isothermal near-shore water column due to tidal mixing (Bailey, MacGregor, & Hachey, 1954). Temperatures at 100–200 m remain between 2–4°C year round (Garrett, Keeley, & Greenburg, 1978).

Minas Basin is a shallow, summer-warm (16–22°C) marine embayment cul-de-sac with extreme tides (Fig. 1). Tidal amplitudes range from 7 to 16 m (2011–2012 Burntcoat Head Tidal Predictions, Canadian Hydrographic Service). The basin has a maximum depth of 45 m at low water, with tidal currents ranging from 2 to 4 m/s that create a highly turbid environment. Several major rivers flow into the basin, lowering the salinity to 25–30 (Bousfield & Leim, 1959). The extensive intertidal flats (1–5 km wide) support abundant populations of polychaete worms, amphipods, and other macrobenthic life that are food sources for Atlantic Sturgeon (McLean et al., 2013). Minas Passage is the only migration conduit between Minas Basin and the outer BoF (Fig. 1). The passage is a narrow (5 km wide), short (11 km long) and deep (125 m) channel that experiences tidal current speeds between to 4–6 m/s, with extremes to 10 m/s.

### 2.2 | Atlantic sturgeon capture and tagging

Atlantic sturgeon were obtained as bycatch from commercial fishing operations which used intertidal fishing weirs or benthic otter trawls in the Minas Basin. Previous studies have described these fishing methods and their relatively low stress and bycatch mortality (Beardsall et al., 2013; McLean et al., 2013). For the present study, sturgeon were captured, measured for FL and total length (TL; cm) and tagged with a uniquely numbered FT-1-94, FLOY® external tag implanted through the periogyte bones on the right side under the dorsal fin. Sturgeon were also tagged on their left side with MK-10 PAT or miniPAT (PSATs) Wildlife Computers, Redmond, WA (Table 1). Only sturgeon >150 cm TL were fitted with MiniPAT tags, which record temperature (range −40 to 60°C; resolution 0.05°C; accuracy ± 0.1°C), depth (range 0–1700 m; resolution 0.5 m; accuracy ± 1% of depth reading), and ambient light level (sensitivity $5 \times 10^{12}$ W $cm^2$ to $5 \times 10^2$ W $cm^2$). PSATs were externally attached through either the dorsal musculature (below the anterior end of the dorsal fin) or through the ridge of the third scute anterior to the dorsal fin because the dorsal musculature attachment caused the tag to collide with the caudal fin on some fish. In each case, one end of a 12 cm, 181 kg test monofilament leader was looped around the release mechanism of the PSAT; the loop was then closed using silver-metal crimps. The other end was wrapped in heat-shrink tubing to protect the fish and leader against abrasion. The wrapped end was threaded through a 0-gauge hollow needle and

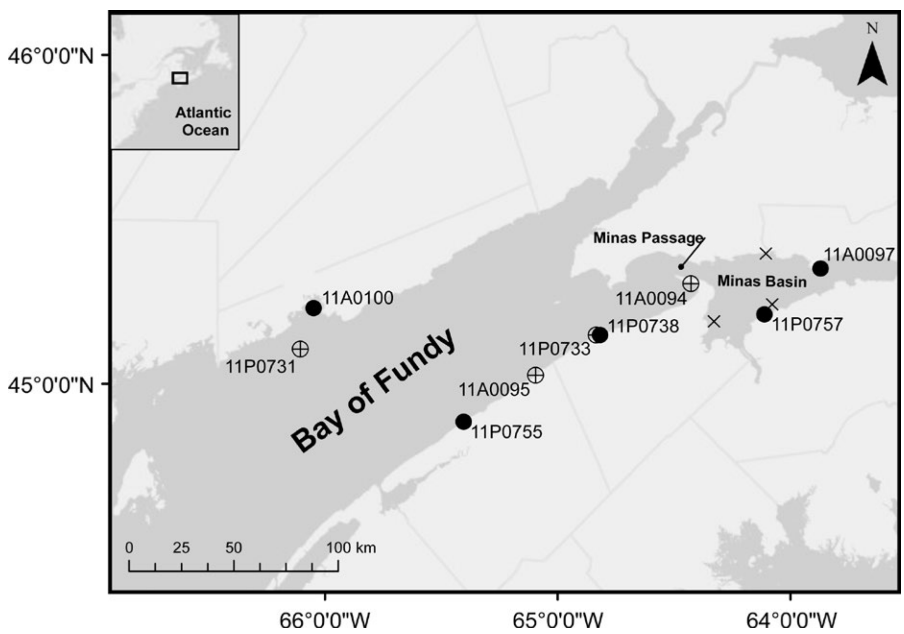


**FIGURE 1** Minas Basin and outer Bay of Fundy, tagging and PSAT pop-off locations (Inset – Atlantic coast of Canada and USA)

**TABLE 1** Sixteen Atlantic sturgeon pop-up satellite archival tag deployments summarized in ascending order of transmission date

| Tag serial number | Fish TL (cm) | Capture method | Deployment date (YYYY-MM-DD) | Programmed release date | Transmission start date | Days at large |
|---|---|---|---|---|---|---|
| 11A0095 | 184 | Trawl | 2011-07-08 | 2012-05-03 | 2012-05-03 | 301 |
| 11A0094 | 172 | Trawl | 2011-07-27 | 2012-05-17 | 2012-05-17 | 295 |
| 11A0097[a] | 202 | Weir | 2012-05-09 | 2013-03-20 | 2012-07-13 | 45 |
| 11P0755[a] | 189 | Trawl | 2012-08-27 | 2013-07-20 | 2012-10-05 | 39 |
| 11P0733 | 175 | Trawl | 2012-08-27 | 2013-06-19 | 2012-10-28 | 62 |
| 11P0731 | 152 | Trawl | 2012-08-22 | 2013-07-29 | 2012-11-29 | 100 |
| 11P0738[a] | 165 | Trawl | 2012-08-22 | 2013-07-23 | 2013-01-26 | 157 |
| 11P0811 | 170 | Trawl | 2012-08-27 | 2013-06-27 | 2013-06-26 | 304 |
| 11A0100[a] | 171 | Trawl | 2012-08-27 | 2013-07-11 | 2013-07-11 | 216 |
| 11P0757[a] | 175 | Trawl | 2012-08-22 | 2013-08-04 | 2013-08-04 | 347 |
| 11A0096 | 171 | Trawl | 2011-07-13 | 2012-05-10 | NA | NA |
| 11A0098 | 203 | Weir | 2012-06-10 | 2013-04-05 | NA | NA |
| 11A0101 | 199 | Trawl | 2012-08-22 | 2013-07-13 | NA | NA |
| 11P0735 | 179 | Trawl | 2012-08-22 | 2013-08-07 | NA | NA |
| 11A0099 | 162 | Trawl | 2012-08-27 | 2013-07-08 | NA | NA |
| 11P0790 | 160 | Trawl | 2012-08-27 | 2013-07-26 | NA | NA |

NA values indicate the PSAT was deployed but did not successfully transmit to ARGOS system thereafter.
[a]Denotes archival data sets.

passed through dorsal musculature then looped; this loop was also closed using silver-metal crimps. In the mid-dorsal scute attachment the wrapped loop was passed through a 0.5 cm diameter hole drilled through the ridge of the scute.

## 2.3 | Data management

Transmitted data means were calculated from histograms provided by Wildlife Computers – Data Analysis Programs software (WC-DAP). Percentages of time spent within a depth or temperature bin were summaries of raw data over 6-hr periods. For calculation of a representative depth for each 6-hr period we summed the products of percentage of time within a bin by the median-value of the bin; a representative depth for 90% of time at 80–100 m depth, and 10% of time at 70–80 m depth was calculated by (0.9 × 90 m) + (0.1 × 75 m). A monthly mean was calculated from those representative depths recorded for the month.

Archival data were the measured depth, temperature, and light values. These data were measured either at user defined intervals (MK-10) or automatically set by tag software (miniPAT). Our archival data were measured every 60 s (MK10) or every 15 s (miniPAT). After recovery these data were summarized to 60-s intervals for analysis. In some instances archival datasets had to be trimmed due to premature release and delayed transmission, sensor malfunction, or extended periods of no-behaviour depth records. Each minute of depth, temperature, or light data were classified into a depth or temperature bin and counted for a 1-month frequency histogram of the deployment period. The count is displayed as a percentage of total data minutes for each month.

## 2.4 | Descriptive statistics

We used non-parametric descriptive statistics to decompose mean hourly depth series for each fish into seasonal variation, depth trend, and non-seasonal variation components using the bfast smoothing function in Rgui 3.0.1. This function has been used to predict phrenological changes in satellite imagery data sets (Verbesselt, Hyndman, Zeileis, & Culvenor, 2010). Ordinary Least Squares residuals-based moving sum was used to identify linear relationships and Bayesian Information Criterion to optimize the location and number of "breaks" (i.e. where local regression parameters significantly changed). Breakpoints indicated a change in Atlantic sturgeon behaviour in either their association with tidal factors or in their depth trends. Minimum length of segments in the trend component corresponded to 1 week of data in the depth time series, thus the component should identify weekly changes in depth trends, if any. Depth trends are relatively long-duration depth changes (e.g. seasonal depth changes); the remainder component represents non-tidal depth variation (i.e. short-duration depth changes from swimming activity). Stacked bar charts were used to descriptively analyze monthly depth and temperature occupancy patterns among archival datasets between each deployment month disregarding the number of days within a month. All data management and analyses were conducted in R 3.0.1 (R Core Team, 2013).

# 3 | RESULTS

## 3.1 | Pop-off locations

Sixteen PSATs were deployed on adult Atlantic sturgeon of 152–203 cm TL (Table 1), and 10 tags reported to ARGOS providing pop-off locations (Fig. 1). All 10 pop-off locations provided by the ARGOS satellite system were in an accurate doppler location precise to 10 m of the tag position at first received transmission. Our satellite tags reported pop-off locations within the Minas Basin or outer BoF, except for one reporting from the mid-Atlantic Ocean. Since Atlantic sturgeon are coastal fish and probably do not migrate to the mid-Atlantic Ocean, the tag most likely released prematurely, failed to activate the prerelease mechanism, and drifted to the mid-Atlantic Ocean before reporting on its programmed day (Stokesbury et al., 2004). Tags released in July and August reported in Minas Basin or approx. 20 km from the mouth of the Saint John River (Fig. 1). Tags reporting during October to February were located close to shore in the outer BoF.

## 3.2 | Overview of data

Of the 10 PSATs reported to the ARGOS satellite system, five were physically retrieved and archival datasets were downloaded. Of the remaining five PSATS, two transmitted useable data and three did not provide useable data. Archival (Fig. 2a) and transmitted (Fig. 2b) datasets show similarities between annual cycles of depth and temperature occupancy from 2011 to 2013. Deepest mean depths were recorded in December for both datasets, although transmitted means were substantially deeper than archival means for that month in particular. Similar minimum temperatures were recorded in March of each year. Archival data suggests low depth variation during summer months and higher depth variation during autumn, winter, and spring months.

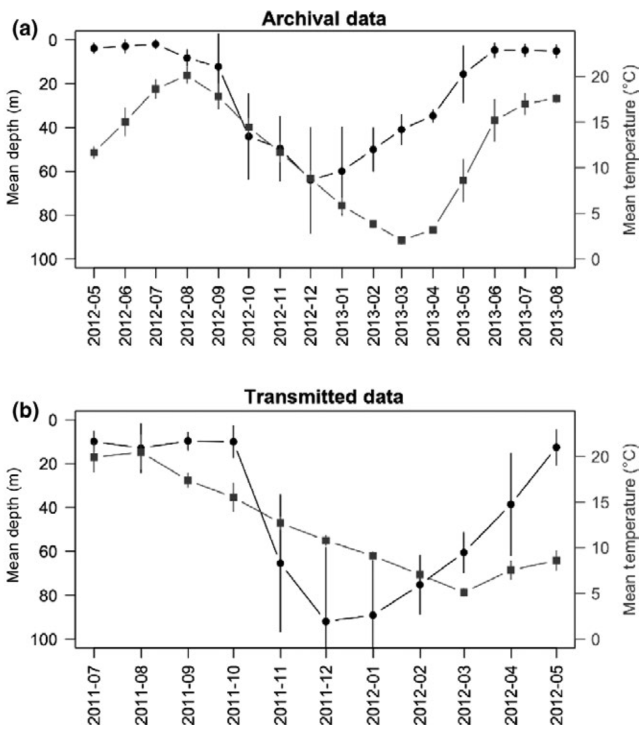


**FIGURE 2** Recovered archival (a) and transmitted (b) PSAT datasets provided monthly mean depth (black circle-line) and temperature (grey square-line) records, May 2011 to August 2013. Error bar length = one standard deviation from the mean

## 3.3 | Collective depth occupancy

All five archival datasets contributed to the collective depth and temperature occupancy (Fig. 2). Depth occupancy was shallowest during May, June, July, and August; 91.0% of the depth records during these months fell within 0–10 m, 8.6% of their depth records fell within 10–20 m, and the remainder of their time was spent at depths 20–40 m. Shallow depth occupancy during this period was recorded in both 2012 and 2013.

In September and October 2012, the recorded sturgeon depth range was from 0 m to greater than 110 m. Three Atlantic sturgeon spent approx. equal proportions of their time during September in 0–20 m depths (14.3%–27.2%), with short durations in 20–30 m depths (0.1%–3%; Fig. 3). Fish 11P0757 spent 48% of September at depths greater than 30 m, and 15% at depths greater than 50 m. In October the sturgeon exhibited a wide range depth occupancy pattern inhabiting depths of 0–90 m. Sturgeon collectively spent 19.4% of October in 30–40 m and 50% of their time in 50–90 m of water. April and May had a similar depth transition; the May 2013 depth record for fish 11P0757 resembled the depth occupancy patterns for all sturgeon recorded in September and October 2012 (Fig. 3).

During winter months tagged Atlantic sturgeon almost always occupied depths in excess of 30 m. Sturgeon maintained depth recordings of >30 m for 99% of November through February 2013, with a bimodal depth distribution between two of the sturgeons (Fig. 3): Fish 11P0757 occupied depths between 20–50 m, whereas fish 11A0100 occupied depths of 40–80 m. During December and January, fish 11P0757 and fish 11A0100 occupied deepest depths with a maximum depth of 119.5 and 113.5 m, respectively. Fish 11A0100 spent 88% of December in depths 80–100 m and 11% in depths 60–80 m, with a mean depth December occupancy of 87.3 ± 6.8 m. Fish 11P0757 spent 97% of December in depths 30–50 m, for a mean depth occupancy of 41.0 ± 4.6 m. In January, fish 11A0100 shifted to 40% in depths 80–100 m and 60% in depths 60–80 m, with a mean depth occupancy of 78.9 ± 9.4 m. Fish 11P0757 depth occupancy remained relatively consistent during January, with 99% spent in depths 30–50 m. During February and March the two sturgeons once again demonstrated an overlap in depth occupancies: they shared 35% of the total time at 40–50 m, and 33% and 22% in depths of 30–40 m and 50–60 m, respectively.

## 3.4 | Collective temperature occupancy

Atlantic sturgeon experienced warmest waters during July and August, particularly in 2012. Data from September 2012 demonstrated a wide range of temperature occupancy, from 12 to 22°C (Fig. 4). Fish 11P0757 entered the coolest waters for the greatest amount of time in September 2012, which corresponds with that fish using greatest depths during the same period. The greatest decrease in mean monthly temperatures occurred between September and October

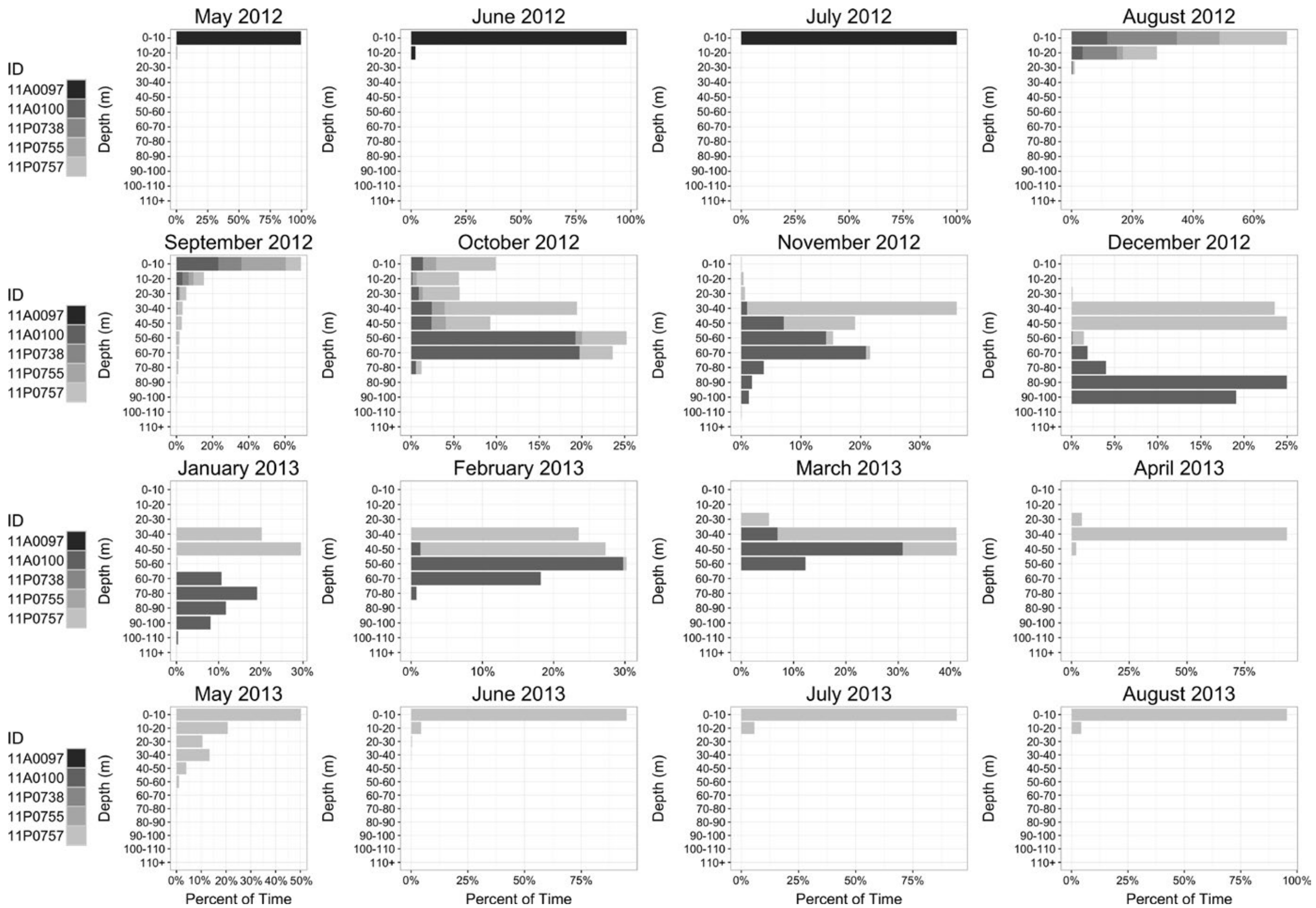


**FIGURE 3** Stacked bar plots representing percent of time tagged Atlantic sturgeon spent within 10 m depth bins for a given month. Bar shading represent different tagged fish. Data are depth records collected every minute of the tag's deployment period

2012 (Fig. 4): temperature occupancy plots revealed a shift from 16 to 20°C in September down to 12–16°C in October. Between October 2012 and March 2013, all fish experienced declining temperatures. During March 2013 Atlantic sturgeon occupied coldest waters; two fish cumulatively spent 46% of their time in 0–2°C water, and the remaining 54% in 2–4°C (Fig. 4). Temperature distributions for individual fish were relatively similar from November 2012 to March 2013 (Fig. 4), despite clear differences in depth occupancy (Fig. 3).

Fish 11P0757 demonstrated stable temperature occupancy during April, then a wide range of temperature occupancy in May and June 2013. Temperature occupancy during April 2012 and January to March 2013 were similar. In May 2013 there was transition from 4–6°C to 10–12°C (Fig. 4). Likewise, in June there was a distinct shift from temperatures <10°C. July 2013 had a similar temperature occupancy pattern as in July 2012, except July 2013 was approx. 2°C cooler. Temperature occupancies in August 2013 were also 2°C cooler relative to August 2012 (Fig. 4).

## 3.5 | Light data

Light-based geolocation is most accurate and precise when the animal carrying the tag is close to the surface in clear waters (Teo et al., 2004). Light-based geolocation estimates often include elliptical error estimates of greater than 1° in both longitude and latitude (1.30° Lat. and 1.89° Long. for Atlantic bluefin tuna *Thunnus thynnus* tagged with PSAT tags (Teo et al., 2004). When animals are in turbid water or occupy deep depths, the light curves are not sufficient for accurate determination of position, particularly in a relatively small geographical area such as the Bay of Fundy. Due to the turbid environment of Minas Basin, the deep depth profiles when tagged sturgeon were in the outer Bay of Fundy, and the small geographical area, light data from PSATs did not provide accurate estimates of positions during tracking.

## 3.6 | Depth time series decomposition

All plots of depth against time clearly demonstrated tidal fluctuation in depth readings (Fig. 5). Decomposition of the mean hourly depth time series with a 24-hr natural time period revealed daily "seasonal" (i.e. tidal) cycles, trends in depth, and an unaccountable variation in depth readings (Fig. 6). "Seasonal" regression components varied between fish and within fish depth time series, which suggests that tidal association was common across Atlantic sturgeon in BoF, but that the association can differ temporally, spatially, intra- and inter-individually (Fig. 6).

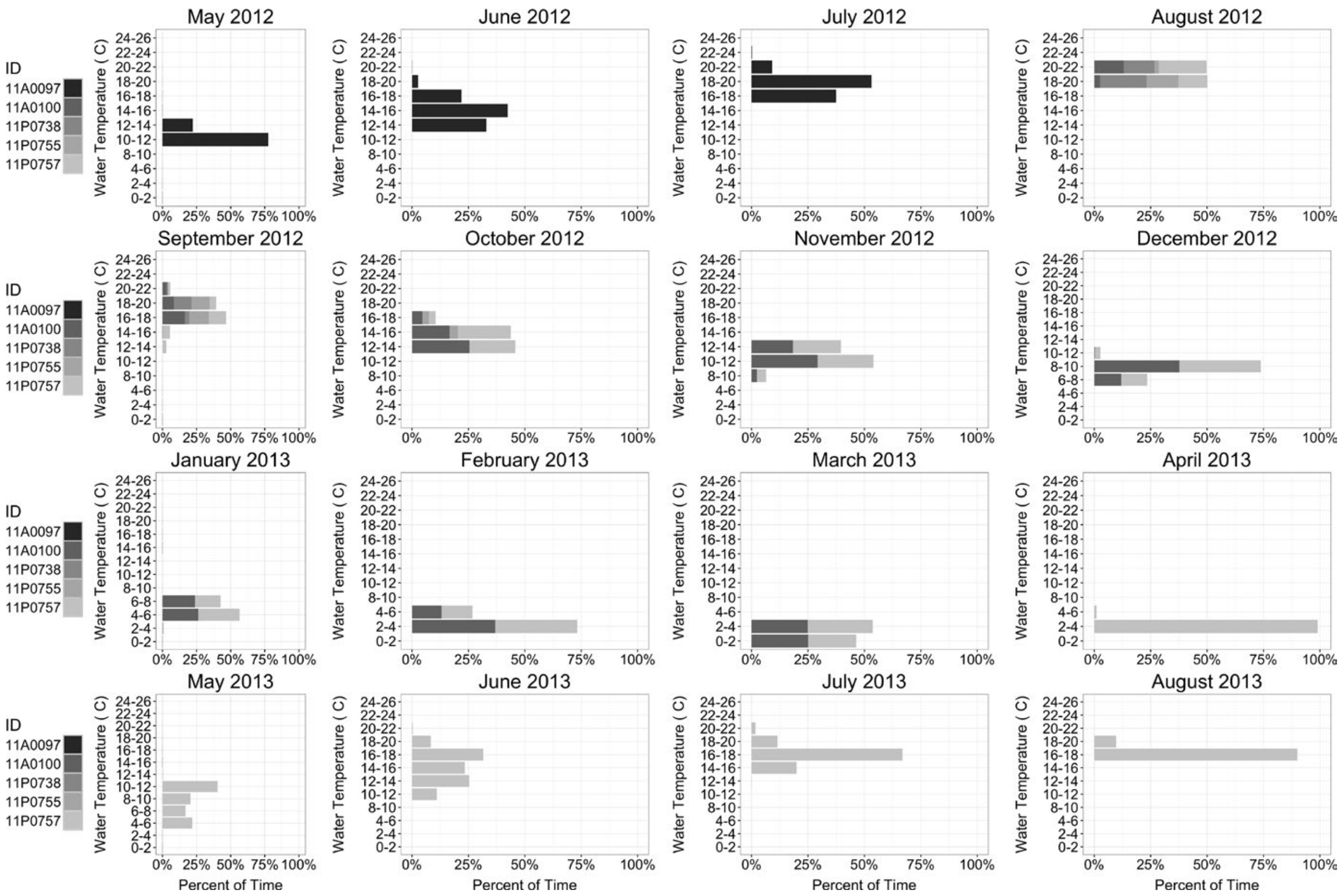


**FIGURE 4** Stacked bar plots representing percent of time tagged Atlantic sturgeon spent within 2°C temperature bins for a given month. Bar shading represent different tagged fish. Data are temperature records collected every minute of the tag's deployment period

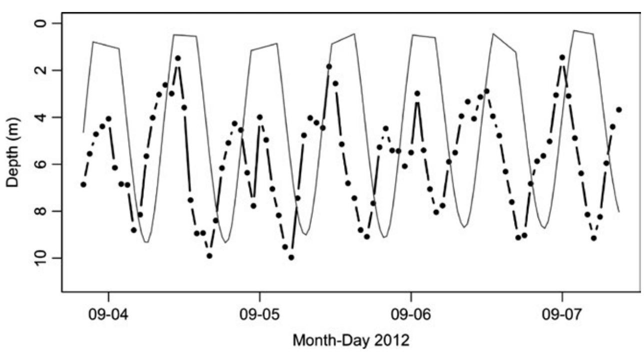


**FIGURE 5** Black dot-line represents an Atlantic sturgeon hourly mean depth. Solid grey line represents tidal water depth height measured from Partridge Island, Nova Scotia using a HOBO® depth sensor moored ~0.5 m above benthic substrate. Straight lines at low tide indicate the depth sensor was exposed during that period

In general, depth trends from May through September were flat linear regression functions. Depth trends during September exhibited abrupt dives followed by a gradual decreasing depth over a weekly time span (Fig. 7), as reported for green sturgeon, *A. medirostris* (Ericson & Hightower, 2007) and Chinese sturgeon, *A. sinensis* (Watanabe et al., 2008) in relation to buoyancy control. Depth trends in October were typically increasing depth functions combined with abrupt dives followed by a weekly decreasing depth function (Fig. 7). November trends were either abrupt decreases in depth followed by increasing depth or flat trends. From December 2012 to March 2013, two sturgeon with archival records demonstrated differing depth profiles. Fish 11P0757 repetitively executed quick depth increases (approx. 10 m) followed by a graduallly decreasing depth throughout December, January, February and March. This "depth step" cycle occurred approx. every 1–2 weeks. During this time fish 11P0757 did not undergo net changes in depth. In contrast, fish 11A0100 descended to deepest waters in early December 2012, and remained at a relatively constant depth until early January. Throughout January 2013 this fish gradually decreased depth; this gradually decreasing depth trend remained relatively stable into March 2013. By March 2013, both fish again inhabited similar depths.

## 4 | DISCUSSION

After aggregating in Minas Basin during summer, Atlantic sturgeon migrated to deeper waters in the outer BoF for winter. Such behaviour is similar to many fishes that utilize the inner BoF during summer. Winter flounder appear in Minas Basin during April to May for

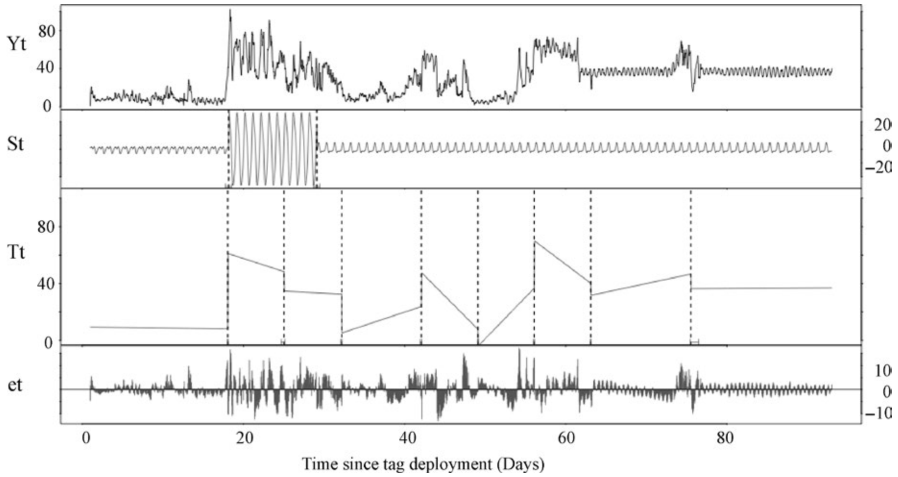


**FIGURE 6** Decomposition of 11P0757 depth time series from deployment date to 22 November 2012 (97 days after deployment). The Yt panel is mean hourly depth data; St panel is seasonal component with breakpoints as vertical dashed line; Tt panel is depth trend component, and et panel is unaccounted depth variance. Response variable is relative contribution to total depth in meters

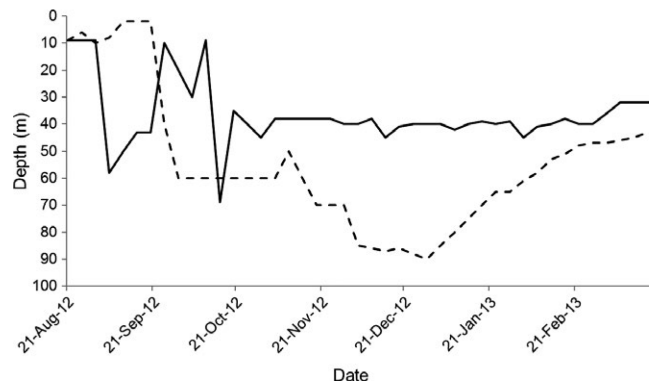


**FIGURE 7** Depth trends from two PSAT-tagged Atlantic sturgeon *Acipenser oxyrinchus* (11P0757, solid black line; 11A0100 broken black line) produced using local regression

spawning and depart the Basin by late summer, to overwinter in the outer BoF or on the Scotian Shelf (McCracken, 1963). American shad arrive in Minas Basin during May and depart by late August, either to migrate south along the USA coast or to overwinter on the Scotian Shelf (Dadswell et al., 1987). Spiny dogfish appear in Minas Basin during May, remain until September, then depart to the outer BoF off southwestern Nova Scotia from October until April (Campana et al., 2008).

All 10 reporting PSATs provided data indicating that Atlantic sturgeon remained in Minas Basin from May until September. From October to January, four tags reported along the southern coast of the outer BoF, and two in outer BoF approx. 20 km from the mouth of Saint John River, NB. These pop-up locations indicated that tagged sturgeon were spending autumn and winter months in the outer BoF, or near a known spawning river. Atlantic sturgeon first return to the Saint John River to spawn at approx. 140 cm TL for males and 160 cm TL for females (C. Ceapa, Acadia Sturgeon and Caviar Inc, unpublished data). Due to this sexual variation in maturity it is not clear if the tagged sturgeon were sub-adults (usually defined as 70–150 cm TL) or adults (usually defined as >150 cm TL; Stewart et al., 2015). One tag, however, reported from the mid-Atlantic Ocean in June 2013. The tag release mechanism likely malfunctioned, with the tag following oceanic currents into the middle of the Atlantic Ocean, as also reported in earlier PSAT tagging studies on the east coast of North America (Stokesbury et al., 2004). The remaining tags first transmitted within Minas Basin during the summer, but archival or transmitted data demonstrated that they had spent the winter months mostly in depths exceeding 50 m and temperatures of 0–4°C, conditions not available in the Minas Basin winter.

Transmitted and archival data indicated that two Atlantic sturgeon staged off the mouth of the Saint John River in July 2013, which suggests that these sturgeon were either preparing for upriver migration, or had recently returned to the marine environment following spawning. These data as well as 22 external tag returns in Minas Basin from Atlantic sturgeon tagged in the Saint John River during their spawning run (C. Ceapa, Acadia Sturgeon and Caviar Inc., pers. comm.) indicate that mature adults inhabit Minas Basin during reproductive recovery years. Additionally, a total of 35 external tags were recovered from Atlantic sturgeon tagged in Minas Basin during the Saint John River spawning run (M. J. Dadswell, unpubl. data), again indicating that mature adults from Saint John River inhabit the Minas Basin during pre-reproductive or reproductive recovery years.

Atlantic sturgeon depth records demonstrated a strong correlation with tidal cycles. The phase, timing, and amplitude of the tidal signature provide excellent qualitative evidence that the Atlantic sturgeon tagged in Minas Basin during summer remained all year in the BoF. Pop-off locations and the maximum depths recorded from all tags were available within the BoF, providing evidence that sturgeon remained within the BoF for the entire deployment period. Six tags did not report to ARGOS satellites, thus we cannot confirm whether those fish remained in BoF using pop-off locations or tidal associations in their depth record.

During summer, Atlantic sturgeon occupied warm waters (15–20°C) and spent more than 90% of their time in shallow depths (0–10 m). These results are similar to Erickson et al. (2011), who found that the Atlantic sturgeon they had tagged occupied mean depths <10 m from April to September. Atlantic sturgeon can tolerate river temperatures above 20°C when spawning (Collins, Smith, Post, & Pashuk, 2000; Erickson et al., 2011); however, those tagged in Minas Basin remained mostly at temperatures of 20°C or less. Water temperatures during summer marine feeding are unlikely constraints on movement, since Atlantic sturgeon survive extended occupancy in warmer river temperatures during spawning runs (Balazik et al., 2012). Instead, we propose that summer temperature occupancy was associated with an optimal foraging habitat (McLean et al., 2013).

Previous PSAT studies reported that Atlantic sturgeon bi-weekly mean depths never exceeded 40 m (Erickson et al., 2011), and that Gulf sturgeon off western Florida overwintered in depths of less than 10 m (Edwards et al., 2007; Ross et al., 2009; Sulak & Clugston, 1999). However, in the outer BoF we found that the Atlantic sturgeon mean monthly overwinter depth distributions ranged from ~40 to ~90 m. These data support reports that Atlantic sturgeon inhabiting high northern latitudes typically encounter trawl fisheries at deeper depths (e.g. 225 cm TL captured at 110 m off New York in the Hudson Canyon; Timoshkin, 1968) relative to low northern latitudes (Stein et al., 2004). Although southern populations of Gulf and Atlantic sturgeon inhabit relatively shallow waters (0–30 m) throughout the year (Fox et al., 2002; Stein et al., 2004), our study demonstrated that Atlantic sturgeon in the BoF commonly occupied depths ranging from 30 to 100 m from early autumn throughout winter and into early spring, probably because this is the depth range where physiologically acceptable temperatures are found (Garrett et al., 1978). Winter flounder and spiny dogfish also overwinter at the same depths and in this same region of the outer BoF (Campana et al., 2008; McCracken, 1963). The deep BoF winter depth occupancy was likely caused by the cold water temperature in shallow depths, particularly in Minas Basin in comparison to more southern locations.

Depth trends calculated from mean hourly depth series provided a variety of depth profiles for Atlantic sturgeon, some of which were seasonally similar. Summer periods were typically flat-line depth trends within the upper 10 m of the water column, usually with an obvious association to tidal fluctuation. Since Atlantic sturgeon are benthic feeders, it is logical to conclude that flat-line depth trends during summer are likely extended periods of benthic association with feeding. September and October depth trends were characterized by relatively large, rapid descending events followed by either gradual or abrupt ascending events. These profiles suggest that Atlantic sturgeon migrated to new environments relative to summer habitat during these months, similar to shortnose sturgeon (Dadswell, 1979) and green sturgeon (Lindley et al., 2008).

Winter depth trend profiles of tagged sturgeon demonstrated two distinct types of overwintering depth activity: "depth stepping" without a net change in mean depth over winter months, and holding at a deep depth followed by gradual decrease. The presence of two different overwinter depth profiles suggests perhaps different overwintering activity, although speculation on these activities is difficult using archival data alone. Geo-referencing archival data records using acoustic telemetry might allow the speculation of physical factors (e.g. bathymetry, coastal rivers, benthos substrate, tidal activity, etc.) influencing depth activity (Fox et al., 2002; Stein et al., 2004).

Transmitted and archival PSAT data provide excellent fishery-independent data that can be used to describe annual cycles in fish behaviour. Our results are the first telemetry results to define Atlantic sturgeon marine depth and temperature occupancy and seasonal movement in their northern range.

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