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ARTICLE

Critical Foraging Habitat of Atlantic Sturgeon Based on Feeding Habits, Prey Distribution, and Movement Patterns in the Saco River Estuary, Maine

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Abstract
An overall lack of information prompted the recent listing of Atlantic Sturgeon *Acipenser oxyrinchus oxyrinchus* under the Endangered Species Act. Key to the restoration of the species and of particular importance is the need to characterize the use of critical habitat across the region, specifically in the Gulf of Maine, where the population was listed as threatened. Much of the research to date has focused on large river systems able to support remnant spawning populations; however, the role of small coastal river systems for Atlantic Sturgeon is not well documented. Several of these systems are being reinhabited, and to facilitate new knowledge about the Gulf of Maine population, a long-term (2009–2014) acoustic telemetry study for 51 Atlantic Sturgeon tagged in the Saco River was evaluated. Results suggested that the majority of fish were aggregating near the natural mouth of the estuary across the 6 years. Gastric lavage samples from 163 (91 juvenile and 72 adult) fish (65.0–171.5 cm fork length) during 2013 and 2014 demonstrated that American Sand Lance *Ammodytes americanus* was the most common prey (the index of relative importance for 2013 and 2014 was 93.5% and 85.4%, respectively), a finding unique to this river system. In addition, benthic sediment grabs, beam trawls, otter trawls, and beach seines conducted in 2013 and 2014 indicated that the distribution of American Sand Lances was comparable to the aggregation area observed for Atlantic Sturgeon. The combined results suggest that the Saco River estuary provides critical foraging habitat imperative for the future recovery of the Gulf of Maine Atlantic Sturgeon population.

The Atlantic Sturgeon *Acipenser oxyrinchus oxyrinchus* is a large, long-lived anadromous fish species that historically supported a major commercial fishery along the eastern coast of the United States (ASSRT 2007). However, due to the combined effects of overharvest, dam construction, and habitat degradation, the species experienced considerable declines in the early 20th century (Smith and Clugston 1997). A coastwide moratorium was established in 1998 in order to rebuild Atlantic Sturgeon stocks, which yielded relatively little success as populations did not rebound as anticipated (ASSRT 2007). To conserve remaining populations, the Gulf of Maine distinct population segment was listed as threatened and the

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New York Bight, Chesapeake Bay, Carolina, and South Atlantic segments were listed as endangered under the Endangered Species Act (NOAA 2012a, 2012b). Despite the recent listing and threatened status, a substantial amount of information necessary for better management of this species remains unknown in the Gulf of Maine distinct population segment (ASSRT 2007). Information characterizing critical habitats for spawning, foraging, and growth remains incomplete and has focused on fish inhabiting larger river systems, such as the Penobscot and Kennebec estuarine complexes (ASSRT 2007; Fernandes et al. 2010; Wippelhauser and Squiers 2015). Smaller coastal systems in the Gulf of Maine, such as the Saco River, have often been overlooked as potential habitats, and they may be critical for the future recovery of Atlantic Sturgeon (ASSRT 2007).

Although the Saco River is the fourth largest river in Maine, the position of the first seaward dam (at river kilometer [rkm] 10, measured from the natural mouth of the river in Saco Bay) presents an impassable boundary for Atlantic Sturgeon, preventing access to the freshwater needed for reproduction. Due to the combination of unsuitable spawning habitat and the historic extirpation of Atlantic Sturgeon prior to the 1980s (Reynolds and Casterlin 1985), the Saco River estuary was not previously considered essential habitat in management regulations. However, after a considerable absence from the Saco River estuary, an Atlantic Sturgeon was captured there in 2007 during a routine trawl survey (Furey and Sulikowski 2011). This finding initiated a study aimed at investigating the possible resurgence of the species and their general usage of the river. Gill-net sampling conducted by Little (2013) from 2008 to 2011 resulted in an average catch per unit effort (CPUE) of 7.64 Atlantic Sturgeon per hour, comparable to that reported for the Kennebec River system for the period of 1998–2000 (CPUE = 7.43; ASSRT 2007). Furthermore, preliminary acoustic telemetry data suggested that Atlantic Sturgeon appeared to be aggregating near the natural mouth of the river with little interannual variation (Little 2013). Initial investigation of stomach contents by Little (2013) determined that this species was feeding exclusively on American Sand Lance *Ammodytes americanus*, a finding contradictory to previous research, which suggests that Atlantic Sturgeon feed primarily on polychaete worms throughout their range (Moser and Ross 1995; Johnson et al. 1997; Haley 1998; Pearson et al. 2007; Savoy 2007; McLean et al. 2013).

These unique observations within the recently reinhabited Saco River estuary suggest that this ecosystem may be providing critical foraging habitat for Atlantic Sturgeon. To expand upon the previous research and further understand the importance of the Saco River estuary, the objectives of this study were (1) to characterize the diet of Atlantic Sturgeon and classify their potential prey distribution within the estuary and (2) to determine whether the movement patterns exhibited by Atlantic Sturgeon were linked to available food resources.

METHODS

Study location.—The headwaters of the Saco River originate in the White Mountains of New Hampshire, and the river empties into the Atlantic Ocean near the southern boundary of Saco Bay (Brothers et al. 2008). Medium to coarse grain sand dominates the sediment composition of the river, which is noted as the main source of sand to the surrounding bay system (Kelley et al. 2005; Brothers et al. 2008). The Saco River estuary is formed by the Cataract Dam, an impassable barrier for Atlantic Sturgeon, located 10 km upstream from the natural mouth (Reynolds and Casterlin 1985). In addition, the mouth of the Saco River is bound by two jetties, which extend the estuary roughly 2.3 km into Saco Bay (Brothers et al. 2008).

Estuarine distribution of Atlantic Sturgeon.—The capture, handling, and tagging of Atlantic Sturgeon conformed with the recommended protocols for the aforementioned sections described in Kahn and Mohead (2010). Fish were captured with bottom-set monofilament gill nets (15.2-cm or 30.5-cm stretch mesh, 2 m high × 100 m long) from May to November in 2013 and 2014. The majority of fishing occurred at slack low tide between the two jetties. Additionally, as part of a larger study surveying the fish assemblage in the Saco River, shorter and smaller stretch mesh gill nets (10.2-cm or 15.2-cm mesh, 2.0 m high × 30 m long) were set at three stations upriver from the jetties, at approximately rkm 3, 5, and 8. Due to a reduced abundance of Atlantic Sturgeon away from the natural mouth, soak times were greater upriver averaging 3.0 h compared with 0.2 h within the jetties.

Following capture, Atlantic Sturgeon were removed from the gill net and placed in a floating holding pen (2.1 × 0.9 × 0.9 m) to minimize stress. After an initial resting period, external morphological measurements, including total length (TL), fork length (FL), head length, interorbital width, and mouth width, were recorded for each individual fish. Individuals were scanned for the presence of an internal PIT tag using an AVID PowerTracker VIII scanner. If no tag was present, fish had a 134.2-kHz PIT tag (model HPT12, Biomark) injected into the base of the dorsal fin and a U.S. Fish and Wildlife Service T-bar tag implanted into the opposite side of the dorsal fin as a secondary mean for identification. When possible, individuals were weighed (0.01 kg) using a Kilotech digital hand scale.

Acoustic telemetry.—A subsample of Atlantic Sturgeon considered to be in the best condition (i.e., no physical trauma present) were selected for acoustic tagging conducted over a long-term project from June 2009 to October 2013. Each Atlantic Sturgeon had an individually coded acoustic tag (model V16; 69 KHz, 16 mm diameter, approximate 2,500-d battery life; VEMCO, Halifax, Nova Scotia) surgically implanted into its abdominal cavity. The transmitter was coated with antibiotic ointment and inserted anteriorly through a 5-cm incision on the ventral surface off the midline of the body. The incision was closed using one or two polydioxanone sutures (PDO II violet monofilament absorbable suture; Oasis, Mettawa, Illinois) and was coated with antibiotic ointment for further protection. The entire surgery lasted approximately 10 min, and the individual was returned to the holding pen to ensure recovery prior to release.

An array of 7 (2009 through 2013) or 11 (2014) stationary acoustic receivers (model VR2W; VEMCO, Halifax, Nova Scotia) were deployed in the lower estuarine portion of the Saco River and in Saco Bay (Figure 1). The maximum detection range for a VR2W receiver is usually between 900 and 1,000 m (VEMCO); therefore, it was assumed that all receivers covered the width of the Saco River estuary as the greatest river width is 330 m (Little 2013). Range testing on individual receivers was not conducted due to time and personnel restraints but should be considered in future studies to ensure assumptions are met. Each year, receivers were deployed in early April or May and data were downloaded from the receivers approximately every 2 months until their retrieval in November or early December. Acoustic data from 2009 to 2011 were initially evaluated to determine the general distribution of Atlantic Sturgeon in the estuary (Little 2013) but were reassessed in this study to include all years in order to obtain a long-term data set. Acoustic detections from 2009 to 2014 were evaluated using a lattice-based home range model modified from Barry and McIntyre (2011). Analyses were performed in R 3.0.2 (R Development Core Team 2014), which generated a 95% general and a 50% core utilization area for all 51 Atlantic Sturgeon. Prior to final analyses, the raw data set was filtered to eliminate simultaneous detections and

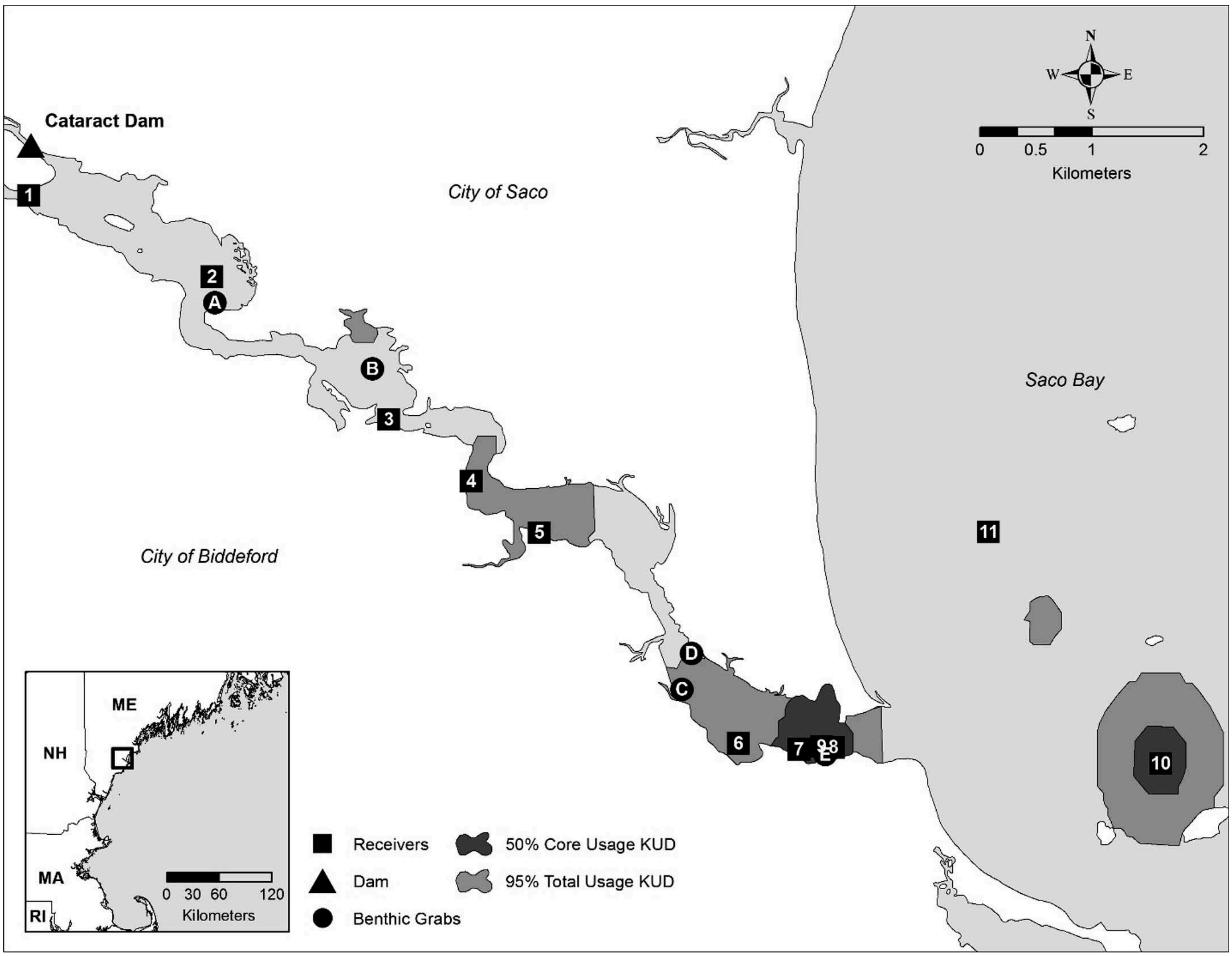

FIGURE 1. Home range analysis of 51 acoustically tagged Atlantic Sturgeon on an array of 11 acoustic receivers from 2009 to 2014 in the Saco River estuary, Maine. The dark shaded regions indicate the 50% core utilization area (i.e., the kernel utilization distribution [KUD]), whereas the light shaded regions indicate the 95% general movement area. Abbreviations of state names in the inset are as follows: ME = Maine, NH = New Hampshire, MA = Massachusetts, and RI = Rhode Island

any detections that did not occur within 60 min of another detection to mitigate the possibility of any false detections.

Stomach collection and analyses.—Stomach contents were collected from Atlantic Sturgeon through gastric lavage, a nonlethal sampling technique modified from Haley (1998) and Brosse et al. (2002). A PVC pipe (1.3 cm diameter × 15.4 cm length) was inserted into the mouth and past the gills of adult Atlantic Sturgeon to aid in guiding a more flexible tube (120 cm long, 9.9 mm inside diameter, 12.7 mm outside diameter), which was slowly inserted through the PVC pipe into the esophagus and then the stomach. Smaller PVC pipe (1.0 cm diameter × 13.6 cm length) and tubing (97 cm long, 6.3 mm inside diameter, 9.7 mm outside diameter) was used for juvenile fish. After the tubing was inserted into the stomach, fish were manually lifted into a vertical position and a 3.1-L garden sprayer was used to gently pump a continuous stream of ambient water into the stomach to dislodge any undigested food. All regurgitated stomach content material was collected on a mesh screen (38.1 × 30.5 cm) and transferred to a labeled bag that was stored on ice in the field for later processing.

In the laboratory, stomach contents were sorted and weighed and all prey items were identified to the lowest taxonomic level possible within 24 h of collection. The index of relative importance (IRI) was used to rank the importance of each observed prey item. This technique combines three different indices, the percent contribution of a prey species by number (%*N*), weight (%*W*), and frequency of occurrence (%*F*), to establish a more comprehensive value on the overall importance of each prey species. The IRI was calculated in this study as follows:

$$\mathrm{IRI} = \%F \times (\%N + \%W),$$

where %*F* is the percentage of stomachs that contained a certain prey species, %*N* is the percentage of the total number of prey items within the stomachs, and %*W* is the percentage of the total weight of prey items in the stomachs. All empty stomachs and any unidentifiable organic material in the stomachs were excluded from analysis (McLean et al. 2013).

Atlantic Sturgeon were grouped into two discrete size-classes to determine if variability occurred in feeding habits between juveniles and adults. Size-classes were based on research conducted by Bain (1997) in which Atlantic Sturgeon ≤135 cm FL were considered immature and fish >135 cm FL were considered adults. A Welch's two-sample *t*-test was performed to determine any differences in the number of unique prey species in the stomach contents of juvenile and adult Atlantic Sturgeon. Analyses were conducted with the statistical computing software R using $\alpha = 0.05$.

Cumulative prey curves were used to determine if a sufficient number of stomach samples had been processed to accurately assess the prey species richness in Atlantic Sturgeon diet in the Saco River estuary (Blanco-Parra et al. 2012). Curves were generated using MATLAB scripts to randomize and iterate the data 120 times to mitigate bias introduced through sampling order. The asymptote of the curve reflects the minimum number of stomach samples needed to accurately characterize the diet (Cortés 1997; Scenna et al. 2006; Pleizier et al. 2012).

Sediment and benthic macrofauna sampling.—Initial analysis by Little (2013) of acoustic telemetry data collected from 2009 to 2011 suggested that Atlantic Sturgeon were aggregating around the natural mouth of the river (rkm 0) to rkm 3.5 (i.e. the core usage area). To investigate potential drivers for this movement, four different sampling techniques were used between May 2013 and October 2014 to determine if prey distribution and sediment type influenced the distribution of Atlantic Sturgeon in the Saco River estuary.

Benthic grabs.—Benthic grab samples were collected at five stations that were designated both inside (n = 3) and outside (n = 2) of the core usage area for Atlantic Sturgeon (Figure 1). Specific sampling site locations in these two areas were assigned based on coinciding Atlantic Sturgeon sampling that also occurred at these locations. At each individual station, predominantly occurring on a weekly basis from June to October 2013, duplicate substrate samples were collected using a 2.2-L ponar grab to assess both the sediment type and benthic macrofauna composition. The mean ± SE depth of grab samples was 2.3 ± 0.11 m and ranged from 0.76 to 5.0 m based on tide and station position. For macrofauna analyses, species data were pooled over time due to the consistency in particular species occurring at the same location as well as to ascertain the complete complex of species at each sampling location for the study. A one-way analysis of variance (ANOVA) was calculated to determine if abundance of a particular species was significantly different outside of and within the core usage area for Atlantic Sturgeon.

Sediment for grain size analysis was collected from the first grab using a 113.4 g polypropylene container to obtain an approximate 100 g sample, with the remaining material discarded. Sediment was analyzed following a modified protocol developed by Manthorp (1995) in which each sample was processed through a series of six decreasing-mesh-size sieves of 4, 2, 0.5, 0.25, 0.125, and 0.058 mm using a Ro-Tap sieve shaker (model RX-94; W.S. Tyler, Mentor, Ohio). The percent contribution of sediment retention on each sieve was weighed to the nearest 0.01 g for each sediment sample (Manthorp 1995; Alfaro 2006). Sediments were then broadly categorized into three grain size-classes: gravel (2–4 mm), sand (0.125–0.5 mm), and silt (0.058 mm), based on the classifications of the Wentworth scale (Wentworth 1922). Sediment that passed through the smallest mesh (0.058 mm) and was not retained by any sieve size was classified as fine material. The four size-classes were used for all subsequent analyses. Additionally, a replicate grab was collected at each station to obtain a complete and representative sample for macrofauna identification.

The entire sample was gently rinsed through a 35-mm-mesh sieve in the field, with remaining material preserved in 70% ethanol and brought back to the laboratory for later classification of benthic macrofauna. Each sample was sorted twice, and all specimens were identified to the lowest taxonomic level possible (Pollock 1998).

Beam and otter trawls.—Five beam trawl (2 m wide and 3-mm mesh) sampling events were performed at sites outside (n = 2) and within (n = 2) the core usage area between June and September 2013. Tow depth ranged from 1.8 to 6.1 m (mean ± SE = 3.1 ± 0.27 m), with a consistent duration of 10 min for each tow. Additionally, a small otter trawl (6 m wide and 25-mm mesh) was used to sample the deeper channel within the jetties over the course of 10 sampling events between May and September 2014. Tow depth ranged from 1.7 to 5.2 m (mean ± SE = 3.2 ± 0.30 m), with a longer duration averaging 14 min.

Beach seines.—As part of the larger study investigating the fish assemblage in the Saco River estuary, a 2-mm-square-mesh beach seine (14 m long and 2 m high) was used to sample one location within the core usage area biweekly between 2010 and 2014. Logistical difficulties (i.e. inaccessibility to sites, steep drop-offs) prevented the use of this gear type at other locations within the Saco River estuary. Replicate seines (each 35 m in length) were conducted for each sampling event. All organisms collected from the beam trawl, otter trawl, and seine were brought back to the laboratory in aerated containers, enumerated, and immediately identified to species level. The numerical abundance of each species was observed between the four gear types and was analyzed based on a presence or absence scale, with relative abundance compared in the core usage area and outside of it.

RESULTS

Estuarine Distribution of Atlantic Sturgeon: Acoustic Telemetry

A total of 51 Atlantic Sturgeon were implanted with acoustic transmitters from 2009 to 2013. Tagged fish ranged in size from 77.0 to 190.4 cm FL with a mean ± SE length of 120.2 ± 4.35 cm FL. All 51 fish were tracked from the initial time of release until the end of the study in November 2014 or when they were no longer detected within the Saco River array. All movement data from tagged individuals were included in the movement analyses. Qualitative preliminary comparisons between the detections recorded by each receiver within the Saco River and Saco Bay array did not show any differences among seasons (i.e. spring [April–June], summer [July–September], and autumn [October–December]).

The number of overall detections by receivers in the mouth of the river (between rkm 0 and rkm 2) were significantly higher than that by the receivers inside of the river (between rkm 2 and rkm 10) (two-sample, two-tailed t-test; P < 0.05). The detection data pooled into the lattice-based home range model, with the addition of the more recent detections, resulted in the same 95% general and 50% core utilization areas from the preliminary study (Little 2013; Figure 1). Atlantic Sturgeon appear to aggregate within the first few kilometers of the Saco River estuary, with overall activity decreasing upriver. The mean ± SE residency time spent in the Saco River was 120 ± 57 d. Atlantic Sturgeon moved into the Saco River estuary in late spring and early summer with a mean ± SE immigration date on June 18 ± 52 d. The highest occurrence of immigration by month happened in May (n = 54) for 25% of Atlantic Sturgeon, followed by June (n = 48) for 23% of Atlantic Sturgeon when looking at movement into the river each year for the combined 6-year period. Additionally, Atlantic Sturgeon were observed emigrating from the Saco River estuary around October 17 ± 32 d. The highest occurrence of emigration by month happened in October (n = 98) for 45% of Atlantic Sturgeon, followed by November (n = 65) for 30% of Atlantic Sturgeon.

Diet Composition

Stomach samples from 163 out of the total 303 captured Atlantic Sturgeon were examined from 43 separate sampling events in the Saco River estuary between 2013 and 2014. The fish selected for gastric lavage ranged in size from 65.0 to 171.5 cm FL (mean ± SE = 123.9 ± 1.98 cm). Gastric lavage indicated 71.8% (117 of 163) of stomachs contained identifiable prey items. American Sand Lances were found to be the primary prey consumed in 2013 and 2014 (mean number = 30.9, 16.5, respectively; range = 1–161, 1–220, respectively) and overall contributed more to the diet in number, weight, and occurrence than any other prey species recovered. Ultimately, American Sand Lances comprised 93.5% of the IRI in 2013 and 85.4% of the IRI in 2014 for all sampled fish (Table 1). There was little difference in the IRI of observed prey species between immature (n = 68) and adult (n = 49) Atlantic Sturgeon (Table 2). In addition, no significant differences were found in the amount of American Sand Lances consumed between juvenile (n = 1,399) and adult (n = 725) Atlantic Sturgeon over the course of the study (two-sample, two-tailed t-test; P = 0.35). Amphipods (family Haustoriidae) were the second most important prey item consumed by Atlantic Sturgeon, accounting for 5.75% (2013) and 12.8% (2014) of the IRI. As with American Sand Lances, there was no significant difference in the amount of Haustoriidae consumed by juvenile (n = 354) and adult Atlantic Sturgeon (n = 318) in the study (two-sample, two-tailed t-test; P = 0.71). All other taxonomic groups comprised less than 1.0% of the IRI in 2013 and less than 2.0% in 2014, indicating that these prey groups are of minor importance in the diet of Atlantic Sturgeon. The cumulative prey curves both exhibited a well-defined asymptote (Figure 2), indicating the total number of stomachs that contained identifiable prey items for juvenile and adult fish was adequate to describe the diet of Atlantic Sturgeon in the Saco River estuary.

TABLE 1. Relative abundance (%*N*), weight contribution (%*W*), frequency of occurrence (%*F*), and index of relative importance (IRI) of prey items consumed by Atlantic Sturgeon (*n* = 117) in the Saco River, Maine, in 2013 and 2014.

	%*N*		%*W*		%*F*		IRI (%)	
Prey item	2013	2014	2013	2014	2013	2014	2013	2014
American Sand Lance *Ammodytes americanus*	82.7	61.0	93.5	90.2	38.8	38.3	93.5	85.4
Amphipod *Gammarus* spp.	2.32	2.82	0.11	0.04	2.50	0.55	0.08	0.02
Amphipod (family Haustoriidae)	11.56	28.1	3.72	3.62	27.5	27.3	5.75	12.8
Sand shrimp *Crangon septemspinosa*	1.38	1.72	1.21	1.17	13.8	11.5	0.49	0.49
Green crab *Carcinus maenas*	0.17	0.10	0.07	0.23	2.50	1.09	<0.01	<0.01
Polychaete worms (family Nereididae)	0.17	3.24	1.19	4.47	2.50	9.84	0.05	1.12
Tube worms (family Spionidae)	0.09	1.31	0.06	0.15	1.25	1.63	<0.01	0.04
Isopod *Cyathura polita*	0.00	0.21	0.00	0.01	0.00	1.09	0.00	<0.01
Isopod *Politolana concharum*	0.00	0.11	0.00	0.04	0.00	1.09	0.00	<0.01
Blue mussel *Mytilus edulis*	0.17	0.94	<0.01	0.04	2.50	4.37	<0.01	0.06
Sea lice (family Caligidae)	1.38	0.42	0.11	<0.01	7.50	3.27	0.15	0.02

Sediment and Benthic Macrofauna Sampling: Benthic Grabs

A total of 120 benthic grabs were used to collect sediment (*n* = 60) and macrofauna samples (*n* = 60) within the estuary. Overall, sand dominated the entire estuary with a higher percentage occurring around the natural mouth of the river. Sediment samples taken closer to the dam had a higher proportion of coarse silt, a much finer grain size (Figure 3). Macrofauna (*n* = 170) obtained through grab samples revealed a distribution difference among the 10 taxa collected within the lower estuary. Tube worms *Spionidae* spp. were the most common benthic organism identified at all stations, with a significantly higher abundance at the two sampling locations outside of the core usage area (one-way ANOVA; $P = 0.032$). Despite this, tube worms were identified in only four Atlantic Sturgeon stomachs and contributed little to the IRI (<0.05%) over the course of the study. In contrast to tube worms, both American Sand Lances and amphipods (family Haustoriidae) were only found within the core usage area, although they were observed at low abundances.

TABLE 2. Index of relative importance (IRI) of prey species in Table 1 for juvenile (*n* = 68) and adult (*n* = 49) Atlantic Sturgeon in the Saco River, Maine, in 2013 and 2014.

	IRI (%)			
	Juvenile		Adult	
Prey item	2013	2014	2013	2014
American Sand Lance	95.7	85.2	87.9	85.1
Amphipod	0.22	0.07	0.00	0.00
Amphipod	3.72	12.3	10.1	13.9
Sand shrimp	0.18	0.72	1.5	0.27
Green crab	0.00	0.00	0.06	0.03
Polychaete worms	0.10	1.43	0.02	0.64
Tube worms	<0.01	0.06	0.00	<0.01
Isopod	0.00	<0.01	0.00	0.00
Isopod	0.00	0.02	0.00	0.00
Blue mussel	<0.01	0.13	0.00	0.04
Sea lice	0.06	0.06	0.42	<0.01

Beam and Otter Trawls

Within the four stations sampled by beam trawl, sand shrimp (also known as sevenspine bay shrimp) *Crangon septemspinosa* was the most abundant species by number (*n* = 586), dominating the total catch composition (73.3%). In addition, the biomass of sand shrimp displayed a progressively increasing trend as sampling moved seaward. Regardless of the large quantity of sand shrimp, this species was infrequent in the stomach samples, accounting for only 0.49% of the IRI for each year. Although American Sand Lances were rarely observed (*n* = 10) in the beam trawl samples, when they were successfully captured they were only found within the core usage area for Atlantic Sturgeon. Otter trawls collected nine additional species that were not observed in either benthic grab or beam trawl methods. In comparison with the aforementioned gear types, fish dominated the catch composition (percent of total catch) of the otter trawl samples, with Atlantic Herring *Clupea harengus* (36.4%), American Sand Lance (16.5%), and Winter Flounder *Pseudopleuronectes americanus* (8.6%) comprising the majority of the tows. Additionally, three Atlantic Sturgeon (104.0, 138.5, and 149.5 cm FL) were captured by otter trawl in 2014.

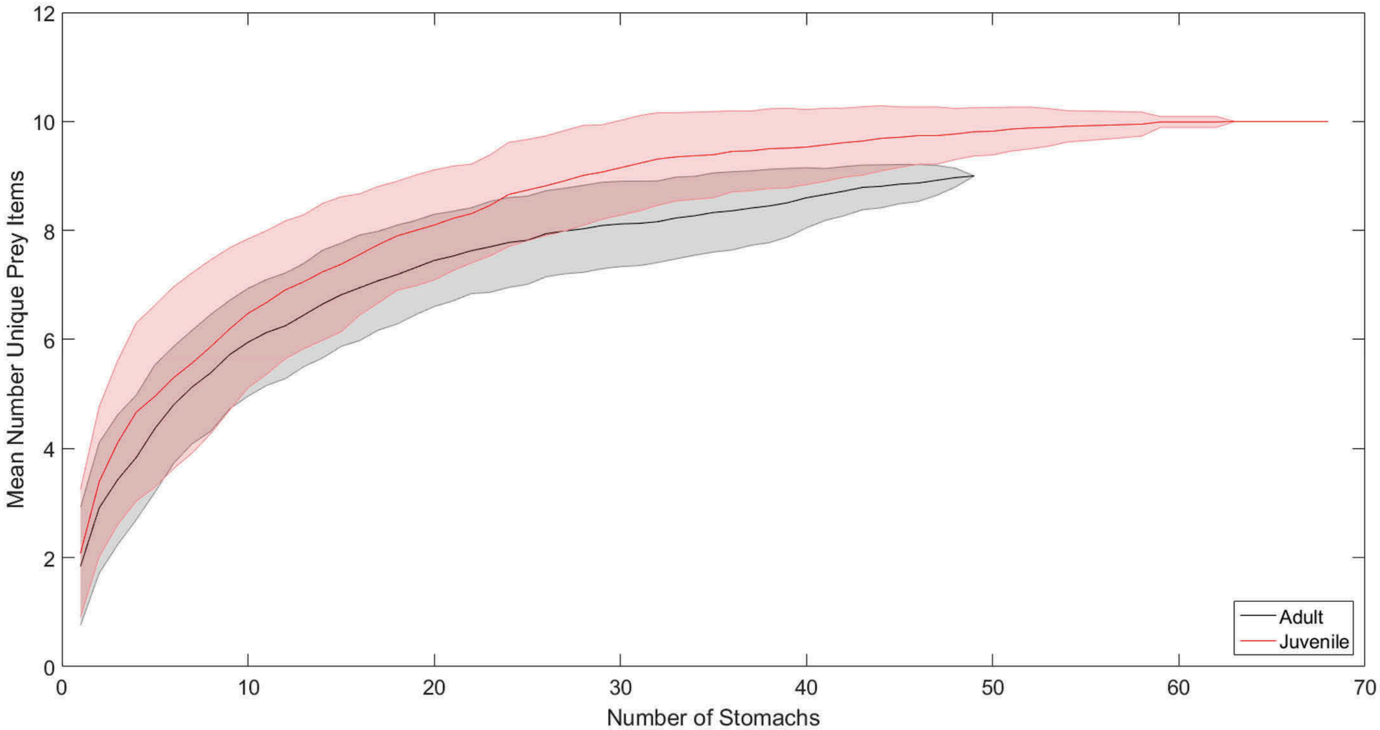

FIGURE 2. Cumulative prey curve for juvenile (n = 68) and adult (n = 49) Atlantic Sturgeon stomachs that contained identifiable prey items. The black and red lines are the mean number of unique prey items after a 120-times randomization order of stomach contents. The shaded regions show the standard deviations.

Beach Seines

Beach seines yielded similar results to the otter trawl with a catch composition primarily dominated by fish species. American Sand Lances were the most abundant species over both years (n = 3,532) and comprised more than a third of the total catch (38.4%) in 2013 and almost half (46.5%) in 2014. Other commonly caught species for 2013 (percent of total catch) included Mummichog *Fundulus heteroclitus* (25.1%), Striped Killifish *Fundulus majalis* (20.1%), and Fourspine Stickleback *Apeltes quadracus* (10%), whereas in 2014, other frequently caught species included Atlantic Silverside *Menidia menidia* (25%), Atlantic Tomcod *Microgadus tomcod* (11.8%), and Atlantic Herring (8.9%).

DISCUSSION

Previous research suggests that Atlantic Sturgeon are opportunistic benthic feeders, primarily foraging on invertebrate species throughout their extensive range (Savoy 2007; McLean et al. 2013). For example, in the Hudson River estuary, Haley (1998) reported that Atlantic Sturgeon fed extensively on polychaete worms, isopods, and amphipods. Similarly, Atlantic Sturgeon sampled from the lower portion of the Connecticut River and Long Island Sound were also described as feeding predominantly on multiple species of polychaete worms (Savoy 2007). Even in the marine coastal waters off New Jersey, the diet of juvenile and adult Atlantic Sturgeon consisted primarily of polychaete worms and isopods, with decapods also contributing a significant portion (Johnson et al. 1997).

Despite the importance of invertebrates in the diet of Atlantic Sturgeon in other ecosystems (Vladykov and Greeley 1963; Moser and Ross 1995; Johnson et al. 1997; Haley 1998; Pearson et al. 2007; Savoy 2007; Dzaugis 2013; McLean et al. 2013), analyses of stomachs collected in the Saco River estuary indicated that Atlantic Sturgeon were primarily feeding on American Sand Lances, an uncommon finding for this species. To better understand this unexplained occurrence, home range analysis of acoustic data combined over a 6-year period suggests that the majority of Atlantic Sturgeon aggregated very close to the natural mouth of the river with little interannual variability. Patterns of immigration and emigration in the Saco River estuary were also shown to be consistent over all consecutive years, but further research should be directed towards a more comprehensive analysis on the individual movement patterns to solidify our spatial and temporal understanding of Atlantic Sturgeon usage of the Saco River estuary. In addition, throughout the current study, American Sand Lances were observed at high abundances at the mouth of the river but were absent upriver of the core usage area for Atlantic Sturgeon. Past studies delineating the fish assemblage of the Saco River estuary support the current

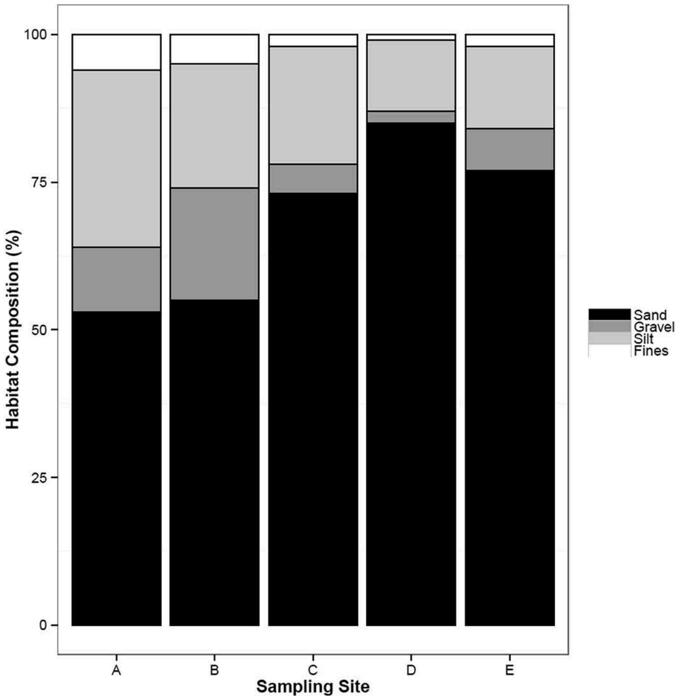

FIGURE 3. Substrate composition based on four discrete particle size-classes within the five sampling stations in the lower estuary of the Saco River (benthic grab locations are shown in Figure 1). Sampling site A represents the location closest to Cataract Dam, with the remaining sites progressively moving seaward. Samples (n = 60) were collected with a 2.2-L ponar grab from June to October 2013 and were sieved to determine particle size.

findings. For example, Reynolds and Casterlin (1985) and Furey and Sulikowski (2011) conducted comprehensive surveys of the vagile macrofauna in the Saco River and each study only observed American Sand Lances in the lower estuarine portion of the river.

Overall, the core usage area appeared to be important habitat not only for an abundance of American Sand Lances but also for a substantial population of Atlantic Sturgeon. In other studies, Atlantic Sturgeon have also shown a preference for a similar substrate habitat. Along the northeastern coast of the United States, Atlantic Sturgeon distribution was inferred from bycatch information combined with both bathymetry and substrate data (Stein et al. 2004). Upon analysis, it appeared that Atlantic Sturgeon were more likely to be found over areas of gravel and sand than soft bottom types. The reasons for these movements remains unknown; however, it is speculated that diet and prey availability are strong factors influencing distribution (Stein et al. 2004). For instance, Gulf Sturgeon *Acipenser oxyrinchus desotoi*, a subspecies of Atlantic Sturgeon *Acipenser oxyrinchus*, show a tendency to aggregate over areas of coarse sand that correspond with known benthic prey resources for sturgeon in the river system (Fox et al. 2002; Harris et al. 2005; Ross et al. 2008). Similarly, Peterson et al. (2013) found that both the physical habitat and related macrobenthic density explained part of the observed Gulf Sturgeon movements. For both species of sturgeon, there appears to be a strong connection between movement and distribution, the availability of prey, and the associated sediment preference.

While the reason for the selectivity towards American Sand Lances in the Saco River estuary remains unknown, several factors could potentially explain this observation. For instance, the relatively low diversity of benthic macrofauna described in this study may have contributed to the population of Atlantic Sturgeon foraging almost exclusively on American Sand Lances. More typical prey items, including polychaete worms and amphipods, were not as abundant within the sampled areas of the Saco River estuary. In contrast, the selectivity for American Sand Lances could be due to the high lipid content of this species, which would yield high energy gains compared with other available prey items in the estuary (Robards et al. 1999). American Sand Lances are thought to achieve a maximum energy content in early summer (Robards et al. 1999), which coincides with the immigration of Atlantic Sturgeon into the Saco River estuary. Nutrient-rich food sources, such as the American Sand Lance, can generate a boost in available energy (Green 2008) that can be important for reproductively active Atlantic Sturgeon that may be passing through this estuary on route to systems able to support spawning populations. Understanding the caloric value of the population of American Sand Lances inhabiting the Saco River estuary, as well as an analysis on the energy allocation in capturing American Sand Lances versus polychaete worms and amphipods, should be considered in future research projects to facilitate the ability to quantify the importance of this forage species in contributing to the growth and overall health of Atlantic Sturgeon utilizing this area.

An additional finding of the current study was the lack of an ontogenetic shift in the diet, which is common for *Acipenser* species. These transitions have been observed to vary between life stages, with a higher diversity of prey consumed by larger size-classes. For example, young-of-the-year Atlantic Sturgeon in the St. Lawrence estuary showed a preference for gammarids, while both juvenile and subadult fish fed on a diet dominated by oligochaetes (Guilbard et al. 2007). Additionally, the number of prey species increased for subadults compared with both smaller life stages, with the larger fish having a more diverse diet. For Atlantic Sturgeon sampled in the Saco River estuary, the diet of juvenile and adult fish showed considerable overlap, especially between prey species, with no statistical difference in the number of unique prey items consumed by both size-classes. It is possible that due to the high caloric content of American Sand Lances, both life stages of Atlantic Sturgeon are utilizing the most available and nutritionally valued prey resource in the Saco River estuary.

In conclusion, this study offers the first detailed investigation of Atlantic Sturgeon diet in relation to potential prey resources, sediment type, and movement distribution in a recently reinhabited river system. With the majority of research focused on larger river systems, specifically in the Gulf of Maine, the importance of smaller recently reinhabited river systems in the life cycle of Atlantic Sturgeon was previously unknown. The Saco River estuary supports an uncommon food supply, suggesting consideration of this estuary as critical habitat. The present study indicates that a small reinhabited estuary has the potential to provide crucial resources vital to the growth and subsequent survival of the Atlantic Sturgeon population in the Gulf of Maine.

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