Feeding ecology of Atlantic sturgeon, Acipenser oxyrinchus oxyrinchus Mitchell, 1815 on the infauna of intertidal mudflats of Minas Basin, Bay of Fundy

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Summary
A large feeding aggregation of Atlantic sturgeon occupies the inner Bay of Fundy during summer, presumably to forage on the intertidal mudflats. The feeding habits of Atlantic sturgeon were examined during summer 2011 in Minas Basin as description of diet is important for identifying critical foraging areas. Atlantic sturgeon demonstrated an overall preference for sandy tube-dwelling polychaetes (Index of Relative Importance (IRI) = 99.7%). Major prey taxa included Mal- danidae (Clymanella sp., 52.5%) and Spionidae, primarily the species Spio- phanes bombyx (41.0%). Other prey items con- sumed included Phyllodocidae (Etione sp., 2.1%), Nephty- dae (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 Corophiidae and Mysidae. There was no significant difference in the number of prey items consumed and the 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 than others to these foraging fish. Considerable baitworm harvesting occurs during summer months in Minas Basin and could potentially create impacts with sturgeon consumers, both directly through competition for prey items and indirectly through change in sediment and benthic community composition.

Introduction
Atlantic sturgeon Acipenser oxyrinchus oxyrinchus, Mitchell 1815 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 1800s and again in the late 1900s 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 (Trenca et al., 2002; Dadswell, 2006; Kahlne 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 (Department of Fisheries and Oceans [DFO], 2009a). Recently in the Maritime Prov-
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 diets of 10 sturgeon, whereas in habitats located further upstream in freshwater, 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; these are usually small age-0 individuals versus older age classes (Dadswell, 1979; 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 the 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 (Acipenser fulvescens) 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 higher number 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, 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 gueldenstaedtii; Zolotarev et al., 1996) have diets consisting primarily of 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).

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 (Menidia menidia) in Minas Basin revealed that feeding occurred on the ebb tide only, presumably because their benthic prey were made more accessible during sediment turnover in turbulent waters on the flooding tide (Gilmurray and Dabor, 1981). It is currently unknown how Atlantic sturgeon utilize the tidal cycle within Minas Basin.

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 Central Minas Basin provides suitable habitat for many benthic organisms, from mud snails (Ilyanassa obsoleta) to polychaete worms (Westhead, 2005). In particular, the larger soft-shell clams, Mya arenaria, are commercially exploited in this region (Westhead, 2005). 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 and 60 000 individuals m\(^{-2}\) (Bousfield and Leim, 1959; Percy, 2001), and sand tube-building polychaetes such as the bamboo worms (family Malandinae). 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, of which large quantities have been exported to the US for recreational fishing bait since the opening of the fishery in 1985 (DFO, 2009b). Landings of approx. 5 million worms worth $900 000 CAD were reached in 2007 (DFO, 2009b). In Minas Basin, however, Glycera populations have decreased, with certain areas experiencing serial depletion due to the overharvest of potential spawners (DFO, 2009b).

In order to assess the importance of the Minas Basin as a foraging habitat for 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 environment, such as sediment type, to identify essential habitat components for Atlantic sturgeon in the estuarine/marine environment.

Materials and methods

Study area

The Minas Basin, located at the head of the Bay of Fundy, is a shallow estuarine waterbody known for its large semidiurnal tidal range (mean of 11.5 m; max of 16 m) (Fig. 1). Minas Basin is separated into four regions: Minas Passage, Central Minas Basin, Cobequid Bay and Southern Bight (Fig. 1). Much of Minas Basin has depths <25 m at low tide, the exception being Minas Passage, which reaches a depth of 115 m (Bousfield and Leim, 1959). Vertical mixing in Minas Passage by tidal action causes fairly uniform summer temperatures (14-14.4 °C) and salinities (31.2-31.4%) throughout the water column causing Minas Passage and Central Minas Basin to have physical characteristics more similar to a marine environment; whereas Cobequid Bay and the Southern Bight are more estuarine (Bousfield and Leim, 1959). Two rivers, the Avon and Shubenacadie, flow into the Southern Bight and Cobequid Bay, respectively. In the estuarine areas of both rivers, summer temperatures can reach >20 °C and salinities <25%.

Fish sampling and stomach content analysis

Stomach contents were sampled from sturgeon captured during summer (June to August) of 2011 using research-directed trawl fishing in the Southern Bight (Fig. 2). Four trawling expeditions were completed in total at two sites, off King-
sport and Walton. Tow duration was between 40 and 80 min at a depth of 5–10 m below the surface, and were typically conducted at 4 km/h. Benthic tows were conducted using a 24-m box/trawl net, with a stretch mesh size of 14 cm. The net was equipped with modified rock hopper equipment and two 200 kg 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 (Fig. 3) during trawling operations using a revised gastric lavage technique (Brosse et al., 2002). Captured sturgeon were immediately placed in a 180 gallon (ca 680-L) fiberglass tank filled with 50 mg/L of MS222 (3-aminobenzoic acid-ethyl-ester-methane sulfate) and moved to a separate workbench once the anaesthetic took effect (i.e. slowed opercular beats and no reaction to stimulus such as a tail grab). With ventral side up and head...
situated over a 500-μm mesh capturing tray, a medical catheter was carefully manoeuvered through the oesophagus until it had reached the beginning of the first stomach loop. The catheter was securely attached to a 2-L pressurized water tank with a control valve, which delivered a pulsed stream of fresh seawater into the sturgeon digestive tract. Pulse injection of water, followed by gentle massaging of the ventral surface, successfully forced stomach contents out of the mouth and into the collection sieve (Fig. 4). A collection tray was placed below the sieve to catch any sediment or small particles that could slip through the 500-μm mesh. The entire procedure lasted between 3 and 7 min, depending on the size of the fish as well as the amount of food in the gut. Water was pulsed into the digestive tract until it ran clear into the sieve, indicating that all food content had been removed.

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. In lab, samples were sorted, classified and enumerated. 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 using means and standard deviations. Adult Atlantic sturgeon have been known to feed on prey ranging in size over multiple taxa and in various numbers per prey item (Guilbard et al., 2007; Hoover et al., 2007; Nellis et al., 2007). Therefore, to represent the importance of different prey items in the individual diets of sampled sturgeons, items were separated by taxa and pooled. Percent occurrence (%O), mean relative abundance (%N), and percent weight (%W) were determined 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: $\text{IRI} = (N + W) \cdot O$; where $N$ is the percent number of a certain prey item, $W$ is the percent weight, and $O$ is the frequency of occurrence (Kurian, 1977; Hyslop, 1980). Any empty stomach was excluded from this analysis.

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

The degree of gut fullness was calculated using Hureau’s index $\text{Ir}$ (Berg, 1979), where $\text{Ir} = \text{ingested biomass/body weight} \times 100\%$. Because of the extreme tides in Minas Basin, the degree of gut fullness in relation to tidal state and time of day was examined (Gilmurray and Daborn, 1981). Gut fullness was also compared between the two capture locations (Fig. 2).

A Shapiro–Wilk test for $\text{Ir}$ 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, $\text{Ir}$ values were log transformed and an ANOVA was used on 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, contributing more to the diet in occurrence, abundance and weight (Fig. 5). Major taxa consumed by Atlantic sturgeon, as determined by the IRI, were the polychaetes, *Clymanella* sp. and *Spiophanes bombym*. Other polychaetes present were *Eteone* sp., primarily *Eteone trilineata* and *Eteone longa*, *Nephtys* sp., *Neireididae* sp., and *Glyceridae* sp., including the bloodworm, *Glycera dibranchiata*. Crustaceans, including *Corophium* sp. and mysids such as *Neomysis americanus*, played a small role in the Atlantic sturgeon diet. Other species identified in trace amounts included the sand shrimp *Crangon septemspinosus*, the isopod *Chiridotea coecea*, the amphipod *Unciola irrorida*, and an unidentified species of Cumacean (all <0.01%). Trace amounts of fish scales were present in five 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 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 and comprised 50% of the sample wet weight.

There was no significant difference in the number of prey items consumed and fork length of the fish ($F = 2.39$, d.f. = 19, $P = 0.14$), nor number of prey taxa consumed and fork length ($F = 1.14$, d.f. = 19, $P = 0.30$). Gut fullness was...
also not significantly related to size of the fish ($F = 4.12$, d.f. = 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 (Kruskall–Wallis $\chi^2 = 2.51$, d.f. = 2, $P = 0.28$). When tide stage was examined, gut fullness was higher on the ebb tide (median ± SD; Ir = 0.05 ± 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; $U = 35$, $Z = 1.41$, $P > 0.05$, $r = 0.31$).

**Discussion**

Atlantic sturgeon diets in Minas Basin consisted primarily of polychaetes (99.7% IRI). Samples were dominated by the families Maldanidae (the bamboo worms), and Spionidae, primarily the species *Spiophanes bombyx*, both abundant sand tube-building invertebrates in the Minas Basin intertidal mudflats (Glenys Gibson, unpubl. 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 <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. Hicklin and Smith (1984) also reported that polychaete densities were negatively correlated with finer grain size and were more abundant in areas with coarse-medium sand. 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 a sub-species of *Acipenser oxyrinchus oxyrinchus*, revealed that 63.8% of occupied space in the coastal marine environment was over coarse sand and shell fragment bottom type, and that 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 because sturgeon 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 that prey items are sieved out and passed 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 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 showed 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 (Gibbard et al., 2007). We detected no significant difference in fish size and the number of prey items nor difference in number of prey taxa consumed in this study, however this result may be a factor of our limited sample size. Sampled sturgeon represented the sub-adult/adult age-classes, thus 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 occurs during all tide phases. A 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, 1981). Recently, Atlantic sturgeon movements over the Minas Basin intertidal zone were described (McLean et al., 2013). Data revealed that acoustically tagged Atlantic sturgeon followed the tide in and that foraging and searching behaviours continued over the duration of the tide until the fish were forced back into the inner Minas Basin at low tide (McLean et al., 2013). 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 are intertidal polychaete worms, they were likely not feeding during low water when the mudflats were completely exposed.

Lack of sand and organic debris in the gut samples is quite unusual 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 in Atlantic sturgeon stomach samples off the coast of New Jersey. Contrarily, large quantities of plant matter were infrequently consumed by sturgeon in Minas Basin. Most Atlantic sturgeon are thought to ingest organic and inorganic detritus incidentally during the feeding process. Vegetal matter is common in many studies, sometimes reaching 50% in near-shore samples (Guilbard et al., 2007).

Overall conclusive evidence is lacking on whether organic debris 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 the present study, with two of these containing notable amounts of plant material. It is possible that plant material and detritus were not successfully retrieved during the sampling period, however, we assume this was not the case. Rather, limited plant matter in the intertidal zone of Minas Basin, particularly in areas where tube-dwelling polychaetes are most abundant, is a more likely explanation for this low presence in our samples.

Sturgeon digestion rates are poorly understood (Mason and Clugston, 1993; Johnson et al., 1997), thus it is possible that some digestion of prey occurred before preservation and caused an underrepresentation of soft body taxa. However, because many of the prey items retrieved by the gastric lavage technique were still alive, we can assume that these items were recently consumed and thus represent an accurate overview of their diet before digestion. It is possible, however, that under-representation 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 therefore were not extracted during the 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 in freshwater or marine ecosystems (Guilbard et al., 2007). In Minas Basin, Atlantic sturgeon fed on 23 taxa, just slightly higher in diversity than in other studies. However only 12 of the reported taxa had >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 ten by Guilbard et al. (2007). Similarly low taxa diversity was identified in the stomach contents of Atlantic sturgeon in the Hudson and Suwannee river estuaries (Mason and Clugston, 1993; Haley, 1999).

The Atlantic sturgeon is apparently an opportunistic predator of sandy-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 have an effect on 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.

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