Review

Consumption of Atlantic Salmon Smolt by Striped Bass: A Review of the Predator-Prey Encounter Literature and Implications for the Design of Effective Sampling Strategies

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Abstract: The native striped bass (*Morone saxatilis*) population of the Miramichi River, New Brunswick is undergoing an unprecedented recovery while Atlantic salmon (*Salmo salar*) numbers within that system continue to decline. Atlantic salmon smolt depart from the Miramichi system during the striped bass spawning period and it is hypothesized that elevated striped bass abundances will increase encounter rates and predation on smolts. We summarize all available striped bass diet studies occurring within the native range of Atlantic salmon and present a review of the feeding behavior and diet preferences of striped bass before, during, and after their spawning period. The key studies vary in methodologies and interpretability. We present a standardized approach for assessing striped bass predation threats and smolt vulnerability and thus an improved understanding of the species interactions to guide future management in the Miramichi River.

Keywords: Conservation; diet; management; methodology; monitoring; predation; striped bass; Atlantic salmon

1. Introduction

The overlapping native range of striped bass (*Morone saxatilis*) and Atlantic salmon (*Salmon salar*) extends nearly 1500 km from the southern extreme of the Atlantic salmon range in the Hudson River, USA [1] to the northern extreme of the striped bass range in the Saint Lawrence River, Canada [2] (Figure 1). Within this area, ~300 rivers currently support Atlantic salmon populations (either native or re-introduced by stocking) [3,4] and six rivers (Hudson, Kennebec, Saint John, Shubenacadie, Miramichi, and Saint Lawrence) are recognized to support reproducing populations of striped bass [5–7].

Many US Atlantic salmon populations were extirpated by the early 1800s as a result of anthropogenic effects such as dam construction, pollution, and overfishing [8–11]. Remaining US Atlantic salmon populations [3,4] exist largely through the efforts of intensive stocking [12], strict angling regulations (e.g., no retention), and habitat remediations [13] that address the most visible threats to the species. Throughout the Canadian range, wild Atlantic salmon returns persist in numerous rivers, although, in many instances, adult returns are low [14]. Declining Atlantic salmon populations (particularly in the southern species range) has led to extirpated and/or threatened status for the species in several rivers (e.g., those of the Inner Bay of Fundy [15], Merrimack, Kennebec [16]) and numerous additional rivers are failing to meet their conservation targets [12,17]. In response, conservation efforts are now beginning to address many less tangible and wide-reaching ecological threats such as competition from escaped aquaculture origin adults [18], warming waters [19], and predation [20].

One documented Atlantic salmon predator is the striped bass. This species enters their natal rivers in spring to spawn (e.g., [6]) such that their spawning period juxtaposes them both temporally and spatially with the river exodus of Atlantic salmon smolts (e.g., [21]). This period is cited as the greatest occurrence of smolt predation by striped bass (e.g., [20,22]). Although there is limited geographical overlap between striped bass and Atlantic salmon spawning rivers (only six support native populations of both species), the migration of adult striped bass along coastal habitats [23], a preference for river estuaries [24], and frequent forays up coastal tributaries [25] leave no shortage of opportunities for potential predator/prey interactions.

The interaction between striped bass and Atlantic salmon smolts has drawn growing scientific and public attention as many striped bass populations are in a state of recovery [22,26]. As striped bass populations expand in both numbers [27,28] and habitat range (e.g., striped bass are now documented in Labrador [29]), the probability of striped bass encountering and predating on threatened Atlantic salmon is likely to increase. Nowhere is this possibility more apparent than on the Miramichi River, New Brunswick (e.g., [20]). The Miramichi River's Atlantic salmon population has been declining [30] while the striped bass, once harvested to the brink of extinction [31], recovered to a peak of 1–2 million spawners in 2017 [32] following an 11-year moratorium on all striped bass fisheries in 2000 and a 21-year commercial closure [22]. Managers are concerned about species interactions, specifically adult striped bass and salmon smolts, and conflicts among the fisheries they support.

The Miramichi River situation has triggered substantial management debates locally over whether to severely restrict the abundance of one native and recently recovered predator (i.e., the striped bass) in order to protect the Atlantic salmon which has faced a long-term decline. However, it is a bellwether for the other rivers where the two species coexist, especially as the striped bass appears to recover and extend their range across that of declining Atlantic salmon populations. As a first step to support the challenging management environment these two species are creating, we investigated and report on one key potential conflict, which is the potential predation impacts of striped bass on Atlantic salmon smolts. We summarized the known striped bass diet in waters where the species co-exist, the feeding behavior of striped bass during the time of greatest overlap with smolt, i.e., pre-, during-, and post-spawning by striped bass, and proposed a standardization of methods to accurately assess the predation threat for future studies. Our goal was to promote a balanced conservation and recovery of both the striped bass and the Atlantic salmon in the Miramichi and other rivers throughout the overlapping species range.

2. Materials and Methods

Striped bass diet studies conducted within their overlapping range with Atlantic salmon (Figure 1, Figure A1) were compiled and then subdivided into three categories: diet of young-of-the-year (YOY), yearling, and small juvenile <20 cm Fork Length (FL) striped bass (Table A1, Figure 1A); diet of adult, sub-adult, and large, juvenile striped bass >20 cm FL in coastal and marine environments (Table A1, Figure 1A); and diets of adult, sub-adult, and large juvenile striped bass >20 cm FL in rivers supporting Atlantic salmon (Table 1, Figure 1). Striped bass <20 cm that were classified in the first group of studies (*n* = 8) typically occupy warm coastal and estuary habitats [6] and the individuals were deemed too small to consume migrating smolts [33,34]. Striped bass sampled in coastal waters as a part of the second group of studies (*n* = 9) were often sampled during mid-summer in tidal lagoons, from beaches, or offshore and would be unlikely to encounter smolts. No study in either of these two groups documented smolt or salmonid predation (Table A1; Figure 1A). Accordingly, we focused on the third category of studies (*n* = 15) because they included striped bass that were large enough to consume Atlantic salmon smolts in habitats where they could be encountered (Table 1; Figure 1).

Of the 15 studies where predation on smolts was possible, four ([35–37] and a secondary study in [22]) were omitted from the analysis due to the lack or absence of detailed information on sampling locations and diet (Table 1). Two additional studies [38,39] were excluded because they occurred in winter outside the smolt migration period. As a final omission, 13 striped bass (size range

201–275 mm) sampled by Gardinier and Hoff [40] were also excluded as their stomach contents were inseparably pooled with individuals ranging from <76 mm to 200 mm (Table 1). These seven omitted studies reported only one smolt and one parr amongst 3557 collected stomach samples (Tables 1 and 2). The eight remaining studies accurately enumerated and documented to species all food items consumed by sampled striped bass during the presumed smolt out-migration period.
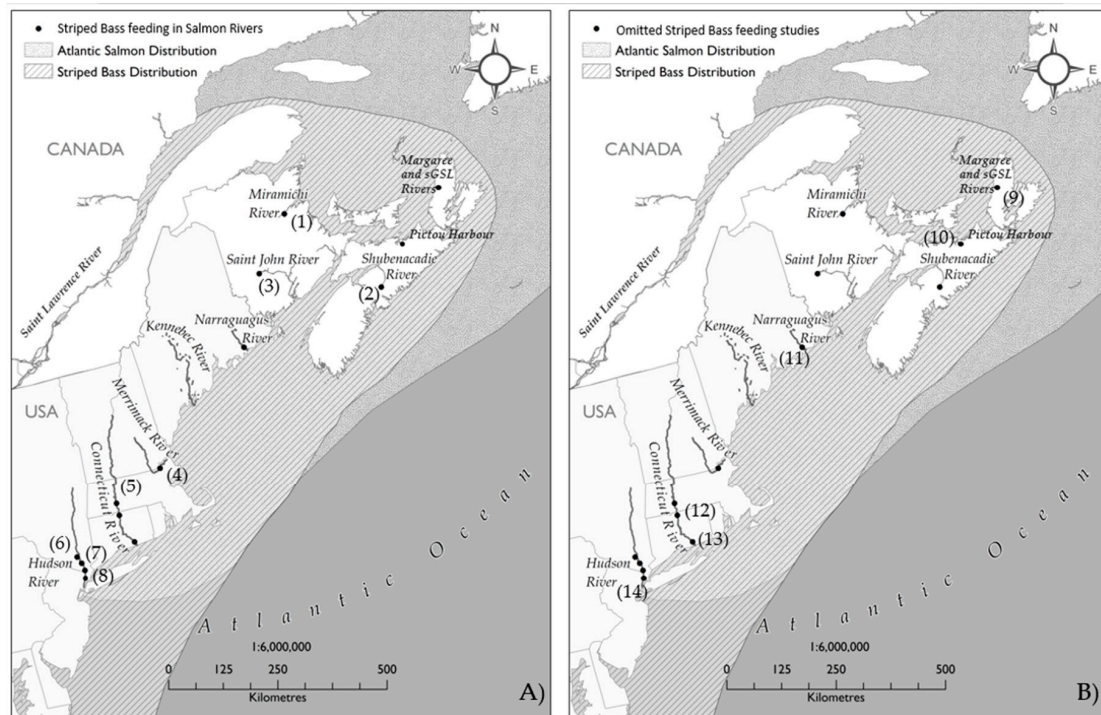

Figure 1. Maps depicting the overlapping range of Atlantic salmon (grey stippled region extending north) and striped bass (grey striped region extending south) along the Atlantic Coast of the United States and Canada. The numbered points on the left panel (**A**) indicate the dietary studies conducted on adult, sub-adult, and large juvenile striped bass > 20 cm Fork Length (FL) in Atlantic salmon supporting rivers (see Table 1). Locations numbered on the right panel (**B**) are studies conducted in the same region that were excluded from our analyses (see omitted studies in Table 1).

Dietary data were extracted from the eight remaining studies and expressed as the frequency of prey (by species) occurrence in stomachs containing food items (Table 2). Frequency of occurrence measures the number of stomachs containing each prey type (species) instead of counting the total abundance of each prey type across all stomachs. Enumerative methods that count each occurrence of each prey type to express dietary proportions (e.g., [22]) risk obscuring the prevalence of individual species of interest or rare species when large numbers of more abundant prey items are present leading to a misrepresentation of diet composition [41,42]. Enumerative methods also fail to account for or misrepresent actual predation rates where the number of predators encountering and predating a specific prey are of interest rather than the proportion of that prey species amongst other dietary items. High frequencies of occurrence may indicate that a prey is utilized by a large proportion of predators, whereas low frequency suggests infrequent predation by a small number of predators [41].

Table 1. Striped bass dietary studies for large adults, sub adults, and large juveniles >20 cm Fork Length (FL) occurring within rivers supporting Atlantic salmon. The number of striped bass stomachs sampled (*n* = 5160), number and proportion of full stomachs (*n* = 1490; 0.16–0.75), collection methods and details, as well as primary food are described. The size ranges of the sampled striped bass are reported from each study as either fork length (FL), total length (TL) or kg. Map numbers (#) match sampling locations illustrated in Figure 1.

Source	Map #	Location	Time of Year/Years	Stomachs Sampled	Full Stomachs	Proportion Full	Collection Method	Evaluation Method	Bass Size Range	Primary Food
Department of Fisheries and Oceans (DFO) [2]	1	Miramichi River	May–June 2013–2015	1844	576	0.31	Angling and trap net	Laboratory dissection	19.2–86.2 cm FL	Rainbow Smelt
Davidson [43]	2	Shubenacadie Lake	12 May–15 September 1950	32	19	0.59	Angling	Angler observation	0.1kg–7.25 kg	Unidentified Fish
Andrews et al. [44]	3	Saint John River	25 April–3 November 2016	244	182	0.75	Angling and fish lift	Gastric lavage	40–117 cm TL	Alosines
Blackwell and Juanes [45]	4	Merrimack River	6–28 May 1997	212	41	0.19	Angling	Gastric lavage	30–78 cm FL	Smolt
Warner and Kynard [46]	5	Connecticut River	25 May–14 June 1982	78	65	0.83	Fish lift	Laboratory dissection	22–44 cm TL	Alosines
Kahnle and Hattala [47]	6	Hudson River	Spring 1990–2006	1859	304	0.16	Electro-fishing, haul sein, gill net	Laboratory dissection	35.6–116.5 cm TL	Unidentified Fish
Dew [48]	7	Hudson River	28 March–20 May (1973–1975)	510	201	0.39	Commercial gill net	Laboratory dissection	>40 cm TL	Blueback Herring
Gardinier and Hoff [40]	8	Hudson River	April–May 1976–1977	380	102	0.27	Haul sein	Laboratory dissection	20–80 cm TL	Unidentified fish
Omitted Due to the Lack of Detailed Information (or Due to the Winter Sampling [2, 6])										
DFO [2] [1]	9	SGLS* River and Coasts	2013–2015	467	219	0.47	Angling and trap net	NA	21.3–73.1 cm FL	Shrimp spp.
Buhariwalla et al. [39] [2]	10	Pictou Harbour	14 January 2013	98	89	0.91	Thermal shock mortalities	Laboratory dissection	11.8–60.2 cm TL	Fourspine Sticklebacks, Striped Bass
Beland [36] [3]	11	Narraguagus River	24 May 2001	1	1	1	Angling	Dissection	34 cm FL	Smolt
Davis et al. [37] [4]	12	Connecticut River	Spring 2005–2007	642	NA	NA	Electro-fishing	NA	~75% >30 cm TL	Blueback Herring
Schulze [35] [5]	13	Connecticut River	Mid-March–mid-December 1994	646	401	0.62	Gill netting	Gastric lavage	>35 cm	Invertebrates and fish

Table 1. *Cont.*

Source	Map #	Location	Time of Year/Years	Stomachs Sampled	Full Stomachs	Proportion Full	Collection Method	Evaluation Method	Bass Size Range	Primary Food
Dunning et al. [38] [6]	14	Hudson River	Winter 1986–1994	1703	814	0.48	Trawl	Laboratory dissection	8.8–66.8 cm TL	*Crangon* spp.
Gardinier and Hoff [40] [7]	8	Hudson River	April–November 1974	13	NA	NA	Beach sein, bottom trawl	Laboratory dissection	20.1–27.5 cm TL	Atlantic Tomcod, Clupeids, White Perch

[1] Department of Fisheries and Oceans (DFO) [2] (secondary study) provides little information on capture locations or prey species, much of the sampling was coastal and smolt would have been unavailable—one parr observed in a striped bass sampled from the Margaree River, N.S. [2] Buhariwalla et al. [39] conducted sampling in winter when smolt would not be present—no smolt observed. [3] Beland's [36] study was a single observation, not a diet study and, therefore, ratios of prey in diets cannot be determined—one smolt observed. [4] Davis et al. [37] only reported consumption of blueback herring—no smolt reported. [5] Schulze [35] did not identify prey to species—no smolt reported. [6] Dunning et al. [38] conducted all sampling during winter—no smolt observed. [7] Gardinier and Hoff [40] sampled 13 striped bass >20 cm but reported stomach fullness collectively with samples from smaller striped bass—no smolts observed. * Southern Gulf of Saint Lawrence (SGSL).

Table 2. Number of sampled striped bass stomachs containing each prey type and the frequency of occurrence of each prey type amongst full stomachs (*n* = 1490). These frequencies were compiled from eight studies of adult, sub-adult, and juvenile striped bass >20 cm Fork Length (FL) totaling 5160 sampled stomachs from rivers supporting Atlantic salmon (see Table 1; refer to Figure 1 for study locations).

Prey Items	Number of Stomachs Containing Prey/1490	Frequency of Occurrence
Rainbow Smelt (*Osmerus mordax*)	357	0.240
Unidentified Alosines (A1)	247	0.166
Alewife (*Alosa pseudoharengus*) (A2)	122	0.082
White perch (*Morone americanus*)	52	0.035
Blueback Herring (*Alosa aestivalis*) (A3)	51	0.034
Atlantic salmon (*Salmo salar*)	**48**	**0.032**
American Eel (*Anguilla rostrata*)	21	0.014
Yellow Perch (*Perca flavescens*)	18	0.012
Atlantic Menhadden (*Brevoortia tyrannus*)	17	0.011
American Sandlance (*Amodytes americanus*)	15	0.010
Atlantic Tomcod (*Microgadus tomcod*)	9	0.006
Sea Lamprey (*Petromyzon marinus*)	9	0.006
Spottail Shiner (*Notropis hudsonius*)	7	0.005
Brown Bullhead (*Ameiurus nebulosus*)	3	0.002
Flatfish (*Pleuronectidae* sp.)	3	0.002
Needlefish (*Belonidae* sp.)	3	0.002
Anchovy (*Anchoa mitchilli*)	2	0.001
Northern Pipefish (*Syngnathus fuscus*)	2	0.001
Moronidae (sp.)	2	0.001
American Shad (*Alosa sapidissima*) (A4)	2	0.001
White Sucker (*Catostomus commersonii*)	2	0.001
White Bullhead (*Ictalurus catus*)	1	0.001
Cunner (*Tautogolabrus adspersus*)	1	0.001
Striped Bass (*Morone saxatilis*)	1	0.001
Atlantic Mackerel (*Scomber scombrus*)	1	0.001
Unidentified fish *	**280**	**0.188**
Non-salmonid Unidentified fish	**89**	**0.060**
Total Alosines (sum A1–A4)	**422**	**0.283**
Fishes (total)	**1365**	**0.916**
Unidentified invertebrates	90	0.060
Insects	49	0.033
Crustaceans	44	0.030
Blue Crab (*Callinectes sapidus*)	41	0.028
Crangon (sp.)	38	0.026
Isopods	35	0.023
Unidentified crabs	10	0.007
Nematodes	11	0.007
Amphipods	7	0.005
Gammarus (spp.)	4	0.003
Polychaetes	5	0.003
Squid	3	0.002
Mud Crab (*Rhithropanopeus harrisii*)	2	0.001
Total Invertebrates	**339**	**0.228**

* *Unidentified fish may include Atlantic salmon smolt and alosines. The frequency of occurrence of Atlantic salmon smolts amongst all sampled striped bass stomachs was 48/5160 = 0.009 , i.e., 0.9% of all sampled striped bass had consumed one or more smolt.*

2.1. Striped Bass Prey Size Selection, Gape Size Limitations, and Smolt Vulnerability

Prey selection by striped bass is influenced both by body size [49] and gape size limitations [50]. Predator size, however, does not scale evenly with prey size selection and larger predators eat both small and large prey [44,51]. Large striped bass may consume smaller prey due to the higher encounter rate and ease of capture [51] in addition to large prey [47]. Smaller striped bass are more limited in the size and species they can consume due to their own physical size. Manooch [33] documented that striped bass consume clupeid prey up to 60% of their body length, but the average prey measured ~20% of bass length.

Smolts originating from the Miramichi River range in size from 11–24 cm FL [34,52]. Based on Manooch [33], a striped bass must be at minimum 18–40 cm FL to predate smolt on the Miramichi River. DFO [22] indicated that striped bass on the Miramichi that consumed smolt were 32.6–62.5 (Scott Douglas, DFO Gulf Region, personal communication) despite sampled striped bass (*n* = 1844) ranging 19.2–86.2 cm FL. Blackwell and Juanes [45] and Beland et al. [36] reported that striped bass consuming smolt were 30–78 cm and 34 cm FL on the Merrimack and Narraguagus Rivers, respectively. These data collectively suggest the smolt vulnerability should be assessed using a minimum threat size for striped bass ≥30 cm FL.

2.2. Feeding Behavior of Striped Bass During the Pre-Spawn, Spawn, and Post-Spawn Periods

Striped bass spawning locations range from just upstream of the head of tide [53] to ~200 km upstream from the river mouth (e.g., Roanoke River, North Carolina; [54]). Spawning occurs from mid-May to mid-June at water temperatures > 14.4 °C with peak egg production occurring from 15.6–19.4 °C [55]. The spawning period generally lasts 1–2 weeks [56,57], can have multiple spawning peaks [56], and male striped bass may occupy spawning grounds longer than female striped bass [57].

Pre-spawn, adult striped bass typically move upstream to stage within the spawning river at or close to their spawning grounds in fresh or mesohaline waters [58,59]. They feed heavily during the upstream migration [60] and may continue to feed actively [40,60,61] or at a reduced rate [22,58,62] as the spawning period approaches. During the pre-spawn period striped bass diets often consist of other anadromous species with overlapping, upstream spawning migrations, e.g., blueback herring (*Alosa aestivalis*) [37], American Shad (*Alosa sapidissima*) [49], Rainbow Smelt [22], and Alewife (*Alosa pseudoharengus*) [44].

Feeding declines leading up to spawning [58,63] and feeding ceases completely directly before and during spawning [6,22,25]. In an early study from the west coast, Scofield [61] reported finding prey in stomachs during the striped bass spawning period, but Raney [64] pointed out that the spawning state of striped bass sampled by Scofield [61] was never evaluated, i.e., sampled fish may not have been mature. Morgan and Gerlach [65] observed no food in the stomachs of female striped bass in spawning conditions in Coos Bay, Oregon, but males at all states of maturity were found to contain food. Striped bass resume feeding immediately post-spawn [65], however, the adult population typically moves rapidly downstream to estuarine or coastal habitats [66] where most feeding has been reported [22,67].

2.3. Documented Predation by Striped Bass on Atlantic Salmon Smolts

Few striped bass diet studies have documented predation on Atlantic salmon smolt. Only Blackwell and Juanes [49], Beland et al. [36], and the DFO [22] made direct observations of Atlantic salmon juveniles (smolt and/or parr) in the diet of striped bass (in the Merrimack, Narraguagus, and Miramichi rivers, respectively).

2.3.1. Blackwell and Juanes 1998: Predation on Atlantic Salmon Smolts by Striped Bass after Dam Passage [45]

Blackwell and Juanes [45] conducted the first diet-based study to raise concerns about striped bass impacts on Atlantic salmon. They sampled 212 striped bass stomachs below the Essex Dam on

the Merrimack River in 1997 (Figure 1, Site 4). Only 19% (*n* = 41) of stomachs contained food items and 70 food items were reported. Of the consumed prey, 46% (*n* = 32) were Atlantic salmon smolt and an additional 40% (*n* = 28) were suspected to be smolt. The remaining 14% of prey were (*n* = 10) were blueback herring, sea lamprey (*Petromyzon marinus*), and other unidentified non-salmonids.

The contribution of Atlantic salmon smolts to the diet of striped bass in Blackwell and Juanes [45] may have been significantly affected by the smolt stocking program and overall state of diadromous fish populations of the Merrimack River at that time. The study was conducted in 1997 when only 403 river herring returned to the Essex Dam fish lift (J. McKeon, US Fish and Wildlife Service, personal communication). Concurrently, 1.8 million juvenile salmon, including 50,000 smolts were stocked to the Merrimack in 1996; 2 million juvenile salmon, including 57,800 smolts were stocked in 1997, and stocking had operated at a similar intensity for at least ten years prior [12]. Blackwell and Juanes [45] stated that all predated smolts to which an origin could be assigned were stocked as fry or smolt. Given the substantial number of stocked smolts and minimal returns of river herring, it is difficult to conclude that the observed striped bass diet in the Merrimack River in 1997 is a true reflection of smolt predation rates under natural river conditions or in other rivers.

Blackwell and Juanes [45] also employed angling to sample striped bass which could have introduced sampling bias due to the gut evacuation during sampling [68] and through the use of lures that resembled smolts [69]. Additionally, the Merrimack River does not support a spawning striped bass population [45] and it is unknown why striped bass entered the river. Elsewhere, non-spawning striped bass enter rivers during spring (i.e., when smolts would be present) to feed [70]. In the Merrimack River study, the proportion of striped bass observed with food in their stomachs (19%) was low among diet studies for the species (range 17–98%; [71]; Table 1, Table A1). The striped bass in the Merrimack River were most probably following the alosine migration upriver or were continuing a learned behavior from times when alosines were abundant (J. McKeon, US Fish and Wildlife Service, personal communication) because these are their preferred prey (Table 2, and see also References [37,44]). With low alosine numbers, the abundance of stocked smolts would produce a high potential striped bass encounter rate on smolts with little alternative prey. Because of the 1997 situation and the lack of additional methodological considerations (e.g., efficiency of gastric lavage), it is challenging to accurately assess the true smolt consumption rates by striped bass and the applicability of the results across the overlapping range of the two species.

2.3.2. Beland et al. 2001: Striped Bass Predation upon Atlantic Salmon Smolt in Maine [36]

Beland et al. [36] documented the consumption of a single, wild Atlantic salmon smolt (18 cm) by an immature striped bass (34 cm FL) on the Narraguagus River, Maine in 1996 (Figure 1, Site 11). Beland et al. [36] recounts how an acoustic signal corresponding to a tagged smolt was suddenly lost when an angler landed a striped bass. This observation was then confirmed via examination of the captured striped bass' stomach contents. The study presented no further evidence of smolt predation and evaluated no additional striped bass stomachs.

2.3.3. DFO 2015: Spawner Abundance and Biological Characteristics of Striped Bass (Morone Saxatilis) in the Southern Gulf of St. Lawrence in 2015 [22]

The Department of Fisheries and Oceans (DFO) [22] sampled 1844 striped bass stomachs (~600) from 1 May to 9 June in each of 2013–2015 by means of angling and commercial alewife fishers (trap nets). Among those striped bass sampled, 32% (*n* = 587) of stomachs contained prey. Five percent (*n* = 28) of the striped bass with prey had consumed smolt, and these 28 individuals collectively consumed 48 smolt (Scott Douglas, DFO Gulf Region, personal communication). In a secondary study, DFO [22] sampled 467 striped bass (21.3–73.1 cm FL) in unspecified locations throughout the Southern Gulf of Saint Lawrence, Miramichi River, NB and Margaree River, NS using angling, index trap nets, and commercial alewife trap nets from 2013–2015. A single Atlantic salmon parr was observed in one striped bass stomach collected from the Margaree River in 2014.

Striped bass and Atlantic salmon in the Miramichi River and its estuary use the two main branches of the river, the Southwest Miramichi (SW) and Northwest Miramichi (NW). Most striped bass spawning has been reported from the NW [32]. DFO [22] sampled 1407 striped bass (76%) from the NW, 114 (6%) from the SW, and 298 (16%) from the main river downstream of both branches (estuarine portion of the river). In addition, 25 striped bass (1%) were either sampled from the NW or the main river during an angling derby. Smolt outmigration numbers for the Miramichi River system tallied 25–35% for the NW and 65–75% for the SW [54]. Such differences in the behavior and habitats of striped bass and Atlantic salmon smolt (between the NW and SW) are important factors when investigating total predation, e.g., smolt numbers were greatest in the SW where striped bass spawning is limited [24].

More than half (54%) of the 48 predated smolt (*n* = 26) in the DFO (2016) study [22] were collected in 10 striped bass stomachs from one location (mouth of Northwest Millstream, a tributary of the NW). This prevalence of smolt-containing stomachs from one location could bias total predation rate estimates if extrapolated for the entire river. For example, differences in the frequency of smolt occurrence in striped bass stomachs between Millstream on the NW (19%) and elsewhere (3%) suggest differential predation rates, i.e., a "predation hot spot" in the Millstream vicinity [72,73].

Sampling methodology can also introduce bias and 54% of sampled striped bass spent approximately 24 h in trap nets prior to gut evacuation [22]. There would have been limited to no access to smolts inside the trap nets and gut evacuation rates at ambient river temperatures are unclear (evacuation of tags by striped bass from tagged prey is 1.2–2.7 days at 23.3 °C; [74]). Striped bass also feed differentially depending on maturity and spawning state (e.g., [40,60]). The sampled striped bass were 19.2–86.2 cm FL and smolts occurred in striped bass 32.6–62.5 cm FL (Scott Douglas, DFO Gulf Region, personal communication). These results are consistent with other reports that suggest prey utilization varies among size and maturity states for striped bass (e.g., [40,75]).

DFO [22] identified an unknown number (described as "many") of the 48 predated smolt based on the occurrence of otoliths in stomach contents of the striped bass. Identifying fish species in diets using otoliths is possible [76], but it can be complicated as otoliths are subject to erosion in the gut [77,78]. Identifying otoliths in diet studies requires protocols that include reference collections and/or atlases to address otolith erosion and double counting [77,79]. For example, DFO [22] reports stomachs with > 1 smolt based on otolith counts but there are three pairs of otoliths per smolt. The residency time of otoliths in striped bass stomachs is also unknown leading to uncertainties regarding smolt origin from either within or exterior to the Miramichi River.

It should be noted within the context of the DFO [22] study, that the objective of the study appears to be the documentation of striped bass diet during their residence in the Miramichi River for spawning. This is very different from a study design that would assess whether striped bass predation affects the declining Atlantic salmon population. This is an important distinction because while DFO [22] reports that smolt contribute to the overall striped bass diet in what can be considered a relatively small proportion, the study cannot address whether the documented removal rate of smolt has an affect on the adult Atlantic salmon population that would be of management concern. To address the question regarding the potential affect, a future study would have to be directly designed to look into that specific question.

2.4. Assessment of Smolt Predation by Acoustic Tagging

The remaining two studies we assessed [20,80] used an analysis of acoustically tagged Atlantic salmon smolt to indicate predation events by striped bass (Figure 2).
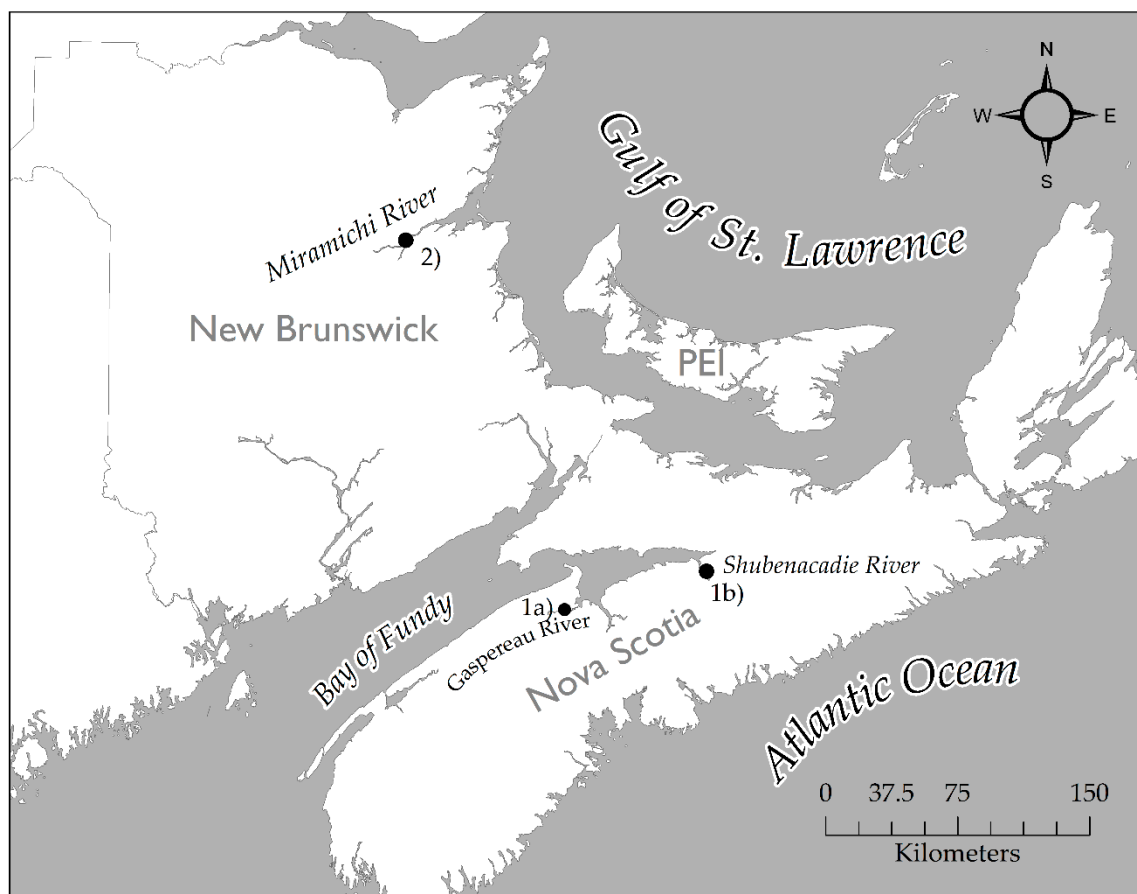
Figure 2. Location of the smolt/striped bass tracking studies conducted by Gibson et al. [80] (1a, b), and Daniels et al. [20] (2) on the Gaspereau/Shubenacadie and Miramichi Rivers, respectively.

2.4.1. Gibson et al. 2015: Effects of Predation on Telemetry-based Estimates: Insights from a Study on Endangered Atlantic Salmon Smolts [80]

Gibson et al. [80] released 93 acoustically tagged "wild acclimated" hatchery origin smolt (originally released as fry) into the Stewiacke River, NS during 2008 (n = 66) and 2011 (n = 27), and released 20 tagged smolts into the Gaspereau River, NS in 2011 (Figure 2). Striped bass (n = 31; TL = 41-89.9 cm) were captured in 2008 and (n = 13; TL = 54.5-78.0) in 2011 in a trap net and tagged with acoustic tags in the upper Shubenacadie River [81] as they exited their overwintering habitat in a large headwater lake. Using cluster analyses based on presumed migration metrics of both species, the study described 2.4–13.6% of smolt movement patterns being most like those of striped bass in the Stewiacke and Gaspereau Rivers across study years. These movement patterns, along with losses of tagged smolt suggested that striped bass predation could have accounted for 7% and 27% of total smolt mortality on the Shubenacadie River in 2008 and 2011, respectively.

The presented results are not a direct measure of predation on wild Atlantic salmon smolt and introduce several biases that could inflate predation rate predictions. The study discussed post-tagging survival but overlooked tag:smolt-length ratios and their impact on smolt behavior (e.g., [82,83]). The tags employed in the study were Vemco V9-6L (W = 2.9 g, L = 24 mm), representing 3.2–14.4% of smolt body weight (range 20–90 g) and 11.4–20.0% of smolt body length (range 120–210 mm FL), exceeding the 8% body weight and 16% body length limits recommended by Lacroix et al. [82], who reported that exceedances significantly impaired the swimming speed of Atlantic salmon juveniles for up to seven days post-tagging. Also, Collins et al. [84] demonstrated that surgical tagging can reduce the average swimming duration for sockeye salmon smolts (*Oncorhynchus nerka*) of similar size. Mortalities attributed to tag size or behavioral consequences suffered by the Atlantic salmon smolt in

Gibson et al. [80] may be reflected in the post-release tagging mortality rates that were 25% (5/20) in the Gaspereau River and 32% (30/93) in the Stewiacke River. Furthermore, there is no accounting of differential predation rates on tagged versus untagged smolt [82,85].

2.4.2. Daniels et al. 2018: Estimating Consumption Rate of Atlantic Salmon Smolts (Salmo salar) by Striped Bass (Morone saxatilis) in the Miramichi River Estuary Using Acoustic Telemetry [20]

Daniels et al. [20] monitored acoustically tagged striped bass and Atlantic salmon smolt on the Miramichi River (Figure 2, Site 1), based closely on the method of Gibson et al. [80]. From 2013–2016, 514 smolts (12.1–18.2 cm FL) were acoustically tagged within the SW and NW branches of the Miramichi River (captured in smolt wheels). In the summer and fall of 2013, 50 striped bass (body sizes were unreported) were angled and tagged in the Bay of Chaleur and 40 striped bass (45.6–73.5 cm FL) were tagged from a DFO index trap net on the SW Miramichi River. Transmitter detections in the Miramichi River were provided by 19 receivers over four years (seven in the NW, five in the SW, and seven in the main river estuary). A random forest model (description in Daniels et al., [20]) was constructed to differentiate predator and prey movements according to eight criteria chosen by the authors. Predation events were based on a binary classification scheme for movement patterns where paths were either "bass like" or "smolt like". Daniels et al. [20] inferred through tag movements that 2–18% of tagged smolts were predated by striped bass annually over a period of four years and specifically, 7–20% of NW origin smolt, and 2–17% of SW origin smolts. The locations of smolt predation were not differentiated between the NW/SW branches and the main stem (downstream of confluence).

2.4.3. Considerations for Acoustic Predation Assessment

Both Daniels et al. [20] and Gibson et al. [80] have several additional caveats that potentially affected their reported predation rates. Both studies tracked striped bass >40 cm, yet it is likely that the "threat size" begins at >30 cm. Describing smolts' movement patterns by transmitter detections at fixed receivers with low spatial coverage i.e., gaps up to 27 km between receivers (e.g., Daniels et al. [20]) and without assessing tagging effects on smolt survival and behavior [82] or detection efficiencies of the fixed receivers can introduce unknown variability in detection rates and, thus, interpretations. For example, detections are predicted to be highly variable in the downstream reaches of the Miramichi River because of its channel and tidal conditions which alter detection rates [86,87]. Also missing is the separation of tagged striped bass among maturity state and pre-, during, and post-spawning activities which affect feeding in striped bass (e.g., [60])

Designating tag behavior as "bass like" also has its limitations in estuaries where multiple smolt predators exist, for example in the Miramichi River where anadromous brook trout (*Salvelinus fontinalis*), adult salmon returning to the sea (i.e., kelts), and seals (e.g., *Halichoerus grypus*) are also present and potentially consume smolt.

3. Discussion

While predation can be a significant driver of fish community structure [88,89], many biotic and abiotic factors regulate the population dynamics of both predators and their prey. In large, complex, and dynamic estuarine ecosystems where striped bass and Atlantic salmon co-occur, like the Miramichi River, quantifying predation and assessing its risk will require the integration of spatial and temporal variables that have the potential to regulate both prey and predators (e.g., [90,91]). For example, in the Miramichi River, the spatial and temporal overlap of the striped bass and Atlantic salmon smolt has received limited study, but these factors are important because they dictate encounter rates, times, and locations. In the Miramichi River, smolt out-migration also overlaps with rainbow smelt, alewife, blueback herring, American shad, and potentially American eel elvers, which are all important foods of striped bass. Other predators may affect predation rates in the Miramichi River, in addition to commercial fishing operations for alewife and smelt which serve as key alternative prey. Assessing

predation in a complex system requires planning and most probably several years to capture the temporal variability among all the relevant factors.

In addition, acoustic tracking data must be interpreted carefully to provide meaningful biological synthesis. Tagged fish may experience mortality and behave differentially after tagging (e.g., [82]) which can alter their survival outcomes and predation susceptibility relative to their untagged counterparts [83]. Fixed receivers have tag detection effectiveness determined by tag-receiver connectivity which is a function of many variables, associated with tags, fish behavior, and environmental conditions [92,93]. Receivers always require testing to determine efficiencies for inclusion in movement models [93].

Studying smolt predation by any predator is inherently complex in nature simply due to the brevity of the smolt migration (i.e., typically less than 4 weeks with the bulk of the smolt migration focused within a few days). This brief time period is rarely conducive to extensive sampling protocols either temporally or spatially rendering most study designs inadequate for the accurate evaluation of predation impacts. Smolt tagging studies likely offer the best and perhaps the only chance to quantify predation during this period but only under the following circumstances: (1) physical and temporal tagging impacts (i.e., swimming impairment and migration delay) must be minimized and tagged smolt must adequately reflect the diversity in size and migratory timing of untagged individuals, and these requirements would likely be achieved through tagging smolt in the fall preceding spring migration; (2) alternative prey abundance during the smolt migration window should be assessed through routine sampling which would separate instances of high smolt predation from low occurrence of alternate forage; (3) the location of predation events of tagged smolt should be compared to the regional and temporal abundance of predators, either from predator tagging or sonar surveys to identify if areas of vulnerability correspond with those of high predator abundance or other riverine features; (4) caveats of tagging (e.g., tag size impacts, delayed release, tagging recovery periods, non-predation mortality) must be clearly outlined by the authors and identified as factors that could result in tagged smolt being less or more susceptible to predation, thus potentially impacting results; and (5) the study should be repeated over multiple years and the results should be compared to smolt escapement, predator abundance and size distribution, as well as subsequent adult salmon returns. Documented predation rates may be inconsequential unless their impact on adult salmon spawner abundance can be demonstrated. Without these considerations, smolt tracking studies may easily overlook critical factors such as predator hot spots or increased prey vulnerability, and may incorrectly assume predation or even high predation across a population or region.

When performing a diet-based analysis of smolt predation, investigators should increase the detail of their reporting, especially when lethal samples are collected. Information on the frequency of occurrence of all prey items, smolt size, predator size, sex and state of maturity, sampling location, sampling time (e.g., hour, day/night) and method of collection should all be reported. These data must also be complemented by a clear delineation of the smolt run timing in the reported sampling season, some measure of the occurrence or abundance of alternative prey species and would benefit greatly from monitoring predator movements through acoustic tagging or sonar survey evaluation. Efforts must also be made to sample a diversity of areas and times and not simply those when predators are most easily captured. The effects of capture method and gear type must also be carefully considered. Diet evaluation studies, however, inevitably risk greatly over or underestimating true predation rates through over or under sampling predation hotspots, especially when predation rates are low. Consequently, diet studies may be best utilized only to identify timing of predation, predation hotspots, predator threat size, and prey size vulnerability, and not to estimate predation rates which may be easily confused with simple diet composition (i.e., prey accessibility/availability and sampling method/location influencing frequency of occurrence). This is especially true when local predator and target prey abundance are unknown during the rapid aggregation and dispersal period associated with spring migrations and spawning.

Additional missing information that could benefit the analysis of striped bass predation on smolt includes: (1) an investigation of striped bass prey digestion rates and residency time of structures or

materials commonly used for prey identification (i.e., otoliths, scales, bones or DNA) in striped bass stomachs, (2) fine scale tracking of predators and prey to determine temporal habitat overlap, and (3) a measurement of adult salmon returns prior to and following documenting levels of smolt predation. More detailed reporting on prey and predator length may further aid in identifying prey vulnerability and predator threat sizes that could be more effectively managed by directed fisheries if necessary.

4. Summary

Few existing studies of striped bass predation on Atlantic salmon smolt collectively provide uncertain interpretations of species interactions and the potential for impacts on salmon populations. Three studies [22,36,45] directly confirm smolt in striped bass stomachs which demonstrate that predation can and does occur. While studies such as the one conducted by the DFO [22] are extensive, they are difficult to interpret because their analyses often overlook complexities associated with methodologies like stomach content analyses and sampling designs (e.g., locations and timing). In addition, there has been no comprehensive study of how predation is effected by the abundance and behavior of prey, other predators, environmental variables (e.g., physical river characteristics, water temperature, tide, light conditions), and the spatiotemporal variation underlying each of these factors. Many of these factors drive or influence the number of smolt observed in striped bass diets and, importantly, total smolt mortality attributed to striped bass predation. Two additional studies [20,80] inferred smolt predation through detections of tagged predators and prey but the biotelemetry techniques used to develop the inferences must be interpreted carefully.

In the future, it is important to focus on designing studies with clear objectives and to differentiate between objectives geared towards documenting the diet of a predator or assessing what impact observed predation levels may be having on a target prey population. This distinction is especially true for the Miramichi River, where a relatively abundant predator may be interacting with a declining prey. An accurate estimate of striped bass predation on Atlantic salmon smolt within a river requires a comprehensive, ecosystem-scale approach. Only careful study of the ecosystem's predators and prey, their spatio-temporal distributions, overlap, behavioral interactions, and relevant environmental drivers will reveal the magnitude and scope of predation Atlantic salmon smolts.

Appendix A

Table A1. Striped bass (*Morone saxatilis*) diet sampling conducted on age 0 and juvenile striped bass and striped bass in coastal or marine environments within the range of Atlantic salmon (*Salmo salar*). For each study itemized below, location and sampling date are provided including the size range of sampled fish, the number of samples taken, the number of stomachs containing food items, and the primary food items identified. Each study can also be located on Figure 1A using the associated map numbers.

Source	Map #	Location	Time of Year/Years	Size of Fish Sampled (mm)/Age	Stomachs Sampled	Full Stomachs	Proportion Full	Primary Food
				Age 0 and Juvenile Striped Bass Diet Sampling				
Robichaud-Leblanc et al. [94]	15	Miramichi River	June–November 1992	2.9–153.3 mm	2928	2247	0.76	Rotifers, Copepods, Mysids, *Crangon*
Smircich et al. [95]	16	Hudson River (near 96 km)	Early June–mid-September 1988–2012	6–60 mm	840	642	0.76	Copepoda, Amphiods (Gammardiae, Corophiidae)
Gardinier and Hoff [40]	17	Hudson River (53–74 km)	April–November 1974	<76 mm	501	422	0.82	Amphipods (*Gammarus*), Copepods and Cladocerans
-	-	-	-	76–150 mm	-	-		Amphipods (*Gammarus*), Bay Anchovy, Atlantic Tomcod, Banded Killifish
-	-	-	-	151–200 mm	-	-		Blueback Herring, Bay Anchovy, Atlantic Tomcod, Banded Killifish, Mummichog
-	-	-	-	201–275 mm	13*	-		Atlantic Tomcod, alosines, White Perch, Striped Bass
Jordan and Juanes [96]	18	Hudson River (35–70 km)	July–November 1994–1997	<50 to >100 mm	695	576	0.82	Amphipods
Howe and Juanes [97]	19	Hudson River (32–72 km)	Mid-July to early November 1998	57.3 ± 10.9 mm	254	231	0.91	Amphipods
Jordan et al. [98]	20	Hudson River (35–70 km)	July–November 1994–1997	<50 to >100 mm	950 **	798	0.84	Amphipods
Curran and Ries [99]	21	Hudson River (Dennings Point)	23 July–13 August	30–110 mm	105	-		Amphipods (*Gammarus*), Chronomids and Copepods
Buckel and Mckown [100]	22	New York Bight	May–November 1997–1998	39–296 mm	602	439	0.72	Sand Shrimp (sp.)
		Total		**2.9–296 mm**	**6193**	**4779**	**0.77**	**77% full stomachs**

<div align="center">Table A1. <i>Cont</i>.</div>

Source	Map #	Location	Time of Year/Years	Size of Fish Sampled (mm)/Age	Stomachs Sampled	Full Stomachs	Proportion Full	Primary Food
				Marine Striped Bass Diet Sampling				
Melvin [101]	23	Kouchibuguac River	15 June–1 November 1978	27.4–54.6 cm	255	179	0.70	Sand Shrimp, *Fundulus*
Rulifson and McKenna [102]	24	Minas Basin, Cobequid Bay	1 June–18 October 1985	69–94 mm	80	78	0.98	*Crangon septemspinosa*
Liem [103]	25	Bass River, Nova Scotia	NA	~20 cm	NA	NA		*Crangon*
Wilkinson [104]	26	Saco Bay, Maine	May–October 2011	43.4–59.9 cm	57	43	0.75	Sand Lance
-	-	-	-	60.0–74.9 cm	-	-		Sand Lance
-	-	-	-	75.0–109.2 cm	-	-		Sand Lance, American lobster
Ferry and Mather [67]	27	Massachusetts estuaries	May–October 1999	37.5–47.5 cm	797	677	0.85	Alosines
Nelson et al. [105]	28	Coastal Massachusetts	June–September 1997–2000	29.0–116.2 cm	3006	1720	0.57	Crustaceans and Atlantic Menhaden
Sagarese et al. [106]	29	Long Island, New York	May–October 2007–2008	39.6–95.9 cm	23	15	0.65	Sand Shrimp, Summer Flounder
Schaefer et al. [75]	30	Long Island, New York	27 April–24 November 1964	27.5–39.9 cm	61	49	0.80	Amphipods and mysids
-	-	-	-	40.0–59.9 cm	183	145	0.79	Amphipods and Bay Anchovy
-	-	-	-	60.0–94.0 cm	123	28	0.22	Amphipods, Bay Anchovy, and Squirrel Hake (*Urophycis chuss*)
-	-	-	-	14.1–24.0 cm	-	-		*Crangon septemspinosa*
-	-	-	-	27.1–36.0 cm	-	-		*Crangon septemspinos*, Unidentified fish
-	-	-	-	38.1–44.0 cm	-	-		*Crangon septemspinos*, Unidentified fish
-	-	-	-	48.1–52.0 cm	-	-		Unidentified fish
Merriman [107] 1941	31	New Jersey, Massachusetts	April–November 1936 and 1937	6.5–115 cm	550	264	0.48	Atlantic Menhaden, Atlantic Silverside
			Total	**6.5–116.2 cm**	**5135**	**3198**	**0.62**	**62% full stomachs**

* Diets of 201–275 mm striped bass sampled by Gardinier and Hoff [40] were inseparable from that of smaller individuals. ** Includes 695 samples from Jordan and Juanes [96].

Species reference: Banded Killifish (Fundulus diaphanus), Bay Anchovy (Anchoa mitchilli), Blueback Herring (Alosa aestivalis), Fourspine Stickleback (Apeltes quadracus), American Lobster (Homarus americanus), Mummichog (Fundulus heteroclitus), Atlantic Menhaden (Brevoortia tyrannus), Sand Lance (Ammodytes americanus), Sand Shrimp (Crangon septemspinosa), Atlnatic Silverside (Menidia menidia notata), Striped Bass (Morone saxatilis), Squirrel Hake (Urophycis chuss) Atlantic Tomcod (Microgadus tomcod), White Perch (Morone americanus).
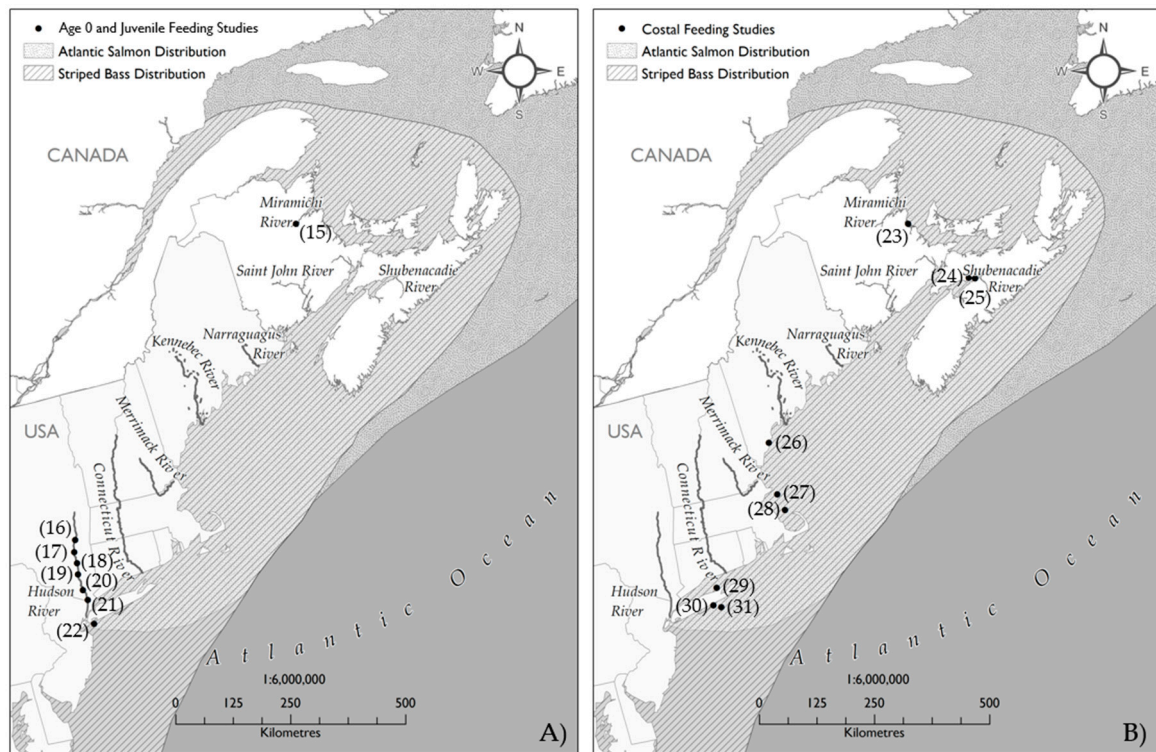

Figure A1. Map depicting the overlapping range of Atlantic salmon (grey, stippled region extending north) and striped bass (grey, striped region extending south) along the Atlantic Coast of the United States and Canada. The numbered points on the left panel (**A**) indicate the dietary studies conducted on age 0 and juvenile striped bass in Atlantic salmon supporting rivers (see Appendix A Table A1). Locations numbered on the right panel (**B**) are studies conducted on striped bass diet in marine and coastal environments across Atlantic salmon range (see Appendix A Table A1).

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