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Using movements and diet analyses to assess effects of introduced muskellunge (*Esox masquinongy*) on Atlantic salmon (*Salmo salar*) in the Saint John River, New Brunswick

R. Allen Curry · Chad A. Doherty · Timothy D. Jardine · Steven L. Currie

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Abstract The muskellunge was introduced in the Saint John River system from stockings in a headwater lake in the 1970s. They have migrated down the system as far as the river's first dam, Mactaquac Hydroelectric Facility, at Fredericton and appear to have established several reproducing populations along the river. This exotic invader represents a potential threat to the severely depleted Atlantic salmon stocks in the river. We radio-tracked muskellunge over a 2-year period in the middle reaches. Home ranges extended to ~100 km in both riverine and lacustrine areas, including 78% of individuals translocated upstream of the dam making their way back through the dam successfully. Downstream of the dam, home ranges were <25 km. No spawning areas were detected. An isotope analyses of diet indicated that the large sub-adults and adults had established the greatest proportion of their biomass in a more ^{15}N depleted environment typical of areas farther upstream. Isotope mixing models could not accurately determine the proportion of Atlantic salmon smolts that may have been consumed by muskellunge, but anadromous salmon had ≤7% probabilities of being in the diet. A bioenergetics model suggested ≤5% of the annual food intake by muskellunge occurs during the smolt out-migration period. For the Saint John River, the impacts of growing numbers of muskellunge are multi-faceted creating a complex management challenge. Muskellunge appear to minimally increase predation risk for Atlantic salmon smolts while their increasing numbers are creating a growing recreational fishery and potential threat to the native fish community and ecosystem.

Keywords Radio and acoustic tracking · Stable isotopes · Modeling diets

R. A. Curry (✉) · C. A. Doherty · T. D. Jardine
Canadian Rivers Institute, New Brunswick Cooperative Fish and Wildlife Research Unit and Stable Isotopes in Nature Laboratory, Biology Department, University of New Brunswick, E3C 6E1 Fredericton, NB, Canada
e-mail: racurry@unb.ca

S. L. Currie
New Brunswick Department of Natural Resources, Region 3, E3E IG3 Islandview, NB, Canada

Introduction

Introduction of non-native species can result in significant changes in ecosystem structure and functions if the introduced species becomes pervasive, displacing and eliminating native species. There are many examples of introduced species becoming invasive in aquatic ecosystems. The Great Lakes of North America have experienced some dramatic changes in structure and function of their ecosystems from introductions of sea lamprey, *Petromyzon marinus*, zebra mussels, *Dreissena polymorpha*, and round gobies, *Neogobious melanostomas*, as described for Lake Michigan (Madenjian et al. 2002). We are learning that effects can begin at any trophic level and then permeate through the entire food web of the ecosystem.

Introductions of large, predatory fish such as *Esox* spp. can significantly impact resident fish communities (e.g., He and Kitchell 1990; Wynne 1995). Introductions of large predators such as muskellunge, *Esox maquinongy*, are generally perceived to create dramatic alterations of ecosystems because their impacts typically occur in the realm of recreational fisheries, i.e., where humans are directly affected. For example, smallmouth bass, *Micropterus dolomieui*, introductions into northeastern North American waters have been correlated with changes in lake trout, *Salvelinus namaycush*, population structure (VanderZanden et al. 1999). The invasion of sea lampreys into lakes Erie, Huron, Michigan, and Superior are strongly correlated with the declines in both recreational and commercial fisheries for lake trout (e.g., Krueger et al. 1995). But introductions are not always negative. Species such as muskellunge, smallmouth and striped bass, *Morone saxatilis*, and Pacific salmon, *Oncorhynchus* spp., are highly prized and can support socially and economically acceptable recreational fisheries after their introduction whether introduced through planned management decisions or illegally (Neal et al. 1999; Simonson and Hewett 1999; Tanner and Tody 2002).

The introduction of muskellunge into a headwater lake of the Saint John River (SJR; Fig. 1) was an unintended expansion of a planned management introduction in the province of Quebec (Stocek et al. 1999). The species is now present throughout approximately 500 km of mainstem and tributary rivers and lakes upstream of Fredericton, NB. Increasing numbers of individuals are being captured in the first fish passage system on the river (Mactaquac Hydroelectric Facility, 20 km upstream of Fredericton; see Fig. 2) and by anglers in the head pond stretching 100 km upstream from there (see for example, http://www.muskiesnb.ca).

The species' impact on the river ecosystem is unknown. The river once supported a large population of wild Atlantic salmon, *Salmo salar*, but numbers have declined to <3,000 returning adults and the population is on the verge of being declared endangered (Jones et al. 2004). With so few salmon in the river, any threat to their survival has raised concerns by angler organizations and agencies responsible for managing the salmon fishery. These groups consider muskellunge to be significant predators of salmon, especially out-migrating smolts and small salmon or grilse returning after one sea winter (Canadian Department of Fisheries and Oceans—DFO and Saint John River Management Advisory Commission, personal communication). There is only one report of *Esox* spp. feeding on out-migrating salmonids in reservoirs (Jepsen et al. 1998). DFO presently destroys all muskellunge captured in their fish traps at all dams along the river.

The continued expansion of muskellunge in the SJR system is a dilemma for fisheries managers. No *Esox* spp. is native to the system (the smaller chain pickerel, *Esox niger*, was introduced in the 1800s) and therefore the muskellunge represents a large, exotic predator with the potential to alter the ecosystem (Townsend 2003). In upstream areas, the ecosystem functions being influenced by muskellunge are unknown, but populations are growing in the river and in several lakes where annual surveys capture age 0+ and 1+ muskellunge (E. LeBlanc, New Brunswick Department of Natural Resources, personal communication). Muskellunge diet, as reviewed by Scott and Crossman (1973), typically consists of three main forage fish: yellow perch, *Perca flavescens*, brown bullhead, *Amerius nebulosus*, and sucker species, *Catostomus* spp., all of which occur in abundance in the SJR (Curry and Munkittrick 2005). Across the muskellunge range, they coexist with many salmonid species, but significantly different habitats most probably restricts interspecific interactions. In the SJR, there is a greater potential for contact between muskellunge and Atlantic salmon because of the salmon's upstream and downstream migrations through cool- to warmwater runs, pools, and reservoirs that are not holding habitats for salmon, but where muskellunge reside. How much contact occurs and

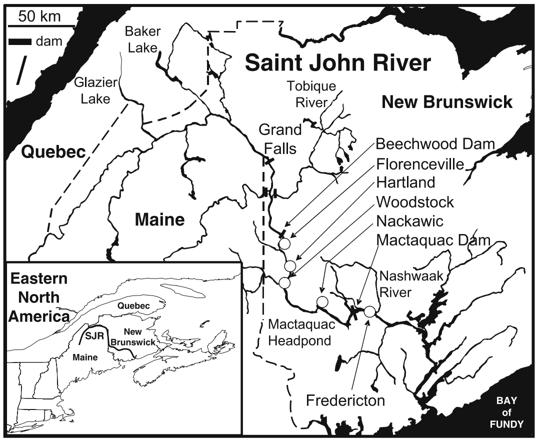

Fig. 1 The Saint John River and landmarks related to muskellunge movements in the middle reach from Florenceville to Fredericton, NB

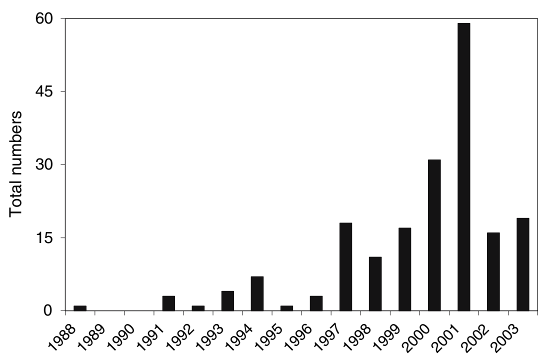

Fig. 2 Total numbers of muskellunge captured annually in the fish trap at the base of the Mactaquac Dam in the Saint John River

whether muskellunge exploit the opportunity to predate Atlantic salmon grilse or smolts is unknown.

Our long-term goal is to determine the impact of muskellunge on the SJR ecosystem. In this study, we continue developing our understanding of their ecology in the river by examining movements and diet patterns in the middle reach of the river where Atlantic salmon smolt production is greatest (Jones et al. 2004). We concentrated on the area downstream of the Mactaquac Hydroelectric Facility, the first dam on the river. Here, the species may have the greatest contact because muskellunge are known to reside in the spillway area of the dam, Atlantic salmon smolts are concentrated and potentially stressed in this area where they have either fallen over the dam or passed through the turbines (there is no fishway), and Atlantic salmon grilse moving upstream are held-up below the dam. Muskellunge predation on Atlantic salmon is potentially greatest in this area.

Study area background

The SJR is >650 km in length with portions of its >55,000 km^2 drainage in Maine, Quebec and New Brunswick (Fig. 1). The fish community consists of >35 species with the greatest diversity downstream of the Mactacquac Dam (Curry and Munkittrick 2005). Muskellunge were stocked as fingerlings multiple times during the 1970s in Lac Frontiere, Quebec (a planned management decision). Muskellunge were first recorded in the system in Maine during the mid-1980s followed by confirmation of the species at the Mactaquac Dam in New Brunswick in 1988 (Stocek et al. 1999). Populations supporting recreational fisheries are established in Glazier and Baker lakes, and the recreational fishery is rapidly expanding at Woodstock (Fig. 1) at the head of the Mactaquac Dam's head pond.

The area used by muskellunge in this study stretched from Fredericton upstream to Hartland, NB (Fig. 1). Fredericton is ~25 km downstream of the Mactaquac Dam where the river is ~1 km wide and up to 3 m deep. From 5 to 15 km downstream of the dam there is a series of large islands creating multiple channels across a 1 km wide channel, but there is only one principle flow channel along the west bank of the river (1–3 m deep). The dam has deep water in its immediate spillway (~3 m) inhabited by many fishes and where a fish trap at the base of the dam is located and operated by Fisheries and Oceans Canada and New Brunswick Power Corporation.

The Mactaquac Dam's head pond stretches 65 km upstream to Woodstock, NB, but the most lacustrine environment extends 30 km upstream to Nackawic, NB (Fig. 1). Upstream of Woodstock is a riverine environment with channel widths from 100 to 200 m and depths up to 2 m. River flow is regulated by the Beechwood Dam upstream of Florenceville, NB, which operates as a daily peaking facility.

Methods

Radio-tagging

Sub-adult to adult muskellunge were taken from the fish trap at the Mactaquac Dam in 2000 (5–24 July) and 2001 (4 July–20 August) and surgically implanted with radio transmitters (Lotek 3-volt micro beeper; 16 mm × 46 mm, 6.7 g). Transmitters, 30 beeps per minute, emitted a frequency of 150–151 MHz, with each tag separated by 20 KHz (minimum battery life of 342 days). Transmitter weight represented less than the 2% of fish mass standard in fish telemetry studies. Fish length ranged from 69.7 to 93.5 cm averaging 83.7 ± 10.5 cm (±1 SD, $n = 18$); weight ranged from 3,000 to 8,450 g averaging 5,470 ± 2,343 g; 50% of muskellunge were females (the largest individuals), 25% males, and 25% immature.

Surgery followed procedures outlined in McKinley and Power (1992) and Curry et al. (2002, 2006). Fish were anesthetized using a clove oil solution of 50 ppm and once loss of equilibrium was reached, a moist V-notched sponge-operating platform was used during tag implantation, to prevent excessive mucus loss. Water flow over the gills was maintained throughout the surgical procedure. An incision, slightly larger than tag diameter was made in the abdomen of the fish approximately mid-way between the pectoral and pelvic girdles. The tag was gently inserted internally into the body cavity, with an external whip antenna fed through an 18-gauge needle, posterior to the incision. Two to four evenly spaced sutures using either a 3–0 or 4–0 needle with non-absorbable black silk were used to close the incision. To ensure incision closure and to help prevent infection, VetBond glue was applied followed by Polysporin antiseptic gel. Three of 6 (2000) and 6 of 12 (2001) tagged fish were released in the reservoir above the dam (≤5 km upstream) and the remainder in the river below the dam (3.5 km downstream).

Attempts to locate fish were conducted on approximately a weekly basis, using either a boat- or truck-mounted multi-element antenna with a Lotek SRX 400 receiver. Detailed notes on fish location in reference to easily distinguishable landmarks were made for calculations of distance traveled. When individuals moved to new locations, we determined exact positions by triangulating signals using different locations. Only individuals tracked successfully for >14 days were used in analyses.

Our tracking data set was not complete enough to produce fine-scale home ranges. We examined locations of individuals in the spring, summer, fall, and winter to determine preferred locations (habitats) within this reach of the river system in distances from the release point (Mactaquac Dam). We define home range as the distance between maximum upstream and downstream locations observed.

Stable isotope analysis

Thirteen muskellunge captured at the Mactaquac Dam during the week of 9 July 2001 and destined for removal from the river were sampled for length, weight, sex (internal verification), and white muscle tissue which provides a good overall representation of assimilated diet (e.g., Hesslein et al. 1993). Tissue samples (~1 g) from the sacrificed muskellunge were excised from above the lateral line and anterior to the dorsal fin. Samples were stored in 95% ETOH until later analyses in the laboratory. Six individuals of all other species captured in the trap were sacrificed and a white muscle sample excised. The samples were supplemented with electrofishing at the dam tailrace to increase sample sizes and species captured.

Tissue samples were dried at 50°C for 48 h and ground into a fine powder with a mortar and pestle. Approximately 0.2 mg aliquots were packed into 3 × 5 mm tin cups. Samples were combusted to gas using a Thermoquest NC 2500 elemental analyzer, and gases were submitted via a continuous flow of helium to a Finnigan MAT Delta Plus isotope-ratio mass spectrometer. Results of $^{13}C{:}^{12}C$ and $^{15}N{:}^{14}N$ isotope ratios were calculated as parts per thousand by the formula

$$\delta X = [(R_{\text{sample}}/R_{\text{standard}}) - 1] \times 1,000$$

where $X = {}^{15}N$ or ${}^{13}C$ and $R = {}^{15}N/{}^{14}N$ or ${}^{13}C/{}^{12}C$.

Values were said to be enriched when more positive than a comparison sample and depleted when more negative. Replicates of commercially available isotope standards yielded results that indicated sample runs were both accurate and precise (International Atomic Energy Agency). Ten percent of the samples were analyzed in duplicate. All analyses occurred at the Stable Isotope in Nature Laboratory, University of New Brunswick.

Stable isotope mixing model

We used the IsoSource mixing model developed by Phillips and Gregg (2003) to estimate dietary source contributions for muskellunge. We used diet-tissue fractionation factors (0.4‰ for δ^{13}C, 3.4‰ for δ^{15}N) from Post (2002) with six possible food sources. The sources were as follows: (1) stream fishes—a pooling of published data from multiple rivers in NB (Jardine et al. (2005)—Miramichi River Atlantic salmon smolts, Little River slimy sculpin, *Cottus cognatus*, Pointe Wolfe River brook trout, *S. fontinalis*; Kelly et al. (2006)—Miramichi River slimy sculpin; Doucett et al. (1996)—Miramichi River brook trout and blacknose dace, *Rhinichthys atratulus*; and, from this study Saint John River Atlantic salmon smolts); (2) adult anadromous fishes at the Mactaquac Dam including alewives, *Alosa pseudoharengus*, blueback herring, *A. aestivalis*, American shad, *A. sapidissima*, and sea lamprey; (3) forage fishes from the vicinity of the Mactaquac dam, including yellow perch, white sucker, *Catostomus commersoni*, and young-of-the-year alosids; (4) forage fishes (yellow perch and white sucker) from Woodstock 60 km upstream from the dam; (5) forage fishes (yellow perch and white sucker) from Hartland 98 km upstream from the dam, and (6) forage fishes (yellow perch and white sucker) from Florenceville 120 km upstream from the dam. These groups were chosen to represent the existing forage fish community within the limits of muskellunge home ranges as estimated from telemetry. We pooled isotope data for species within categories following Phillips et al. (2005), who recommended pooling to reduce the number of sources for modeling provided the pooled sources were isotopically and functionally similar. This was the case in our study, e.g., our mean values for NB stream fishes (δ^{13}C = –27.1 ± 3.3‰, δ^{15}N = 9.6 ± 0.7‰) were consistent with values reported in literature surveys by France (1995a) for lotic fish δ^{13}C (modal value –28‰) and France (1995b) for freshwater fish δ^{15}N (9 ± 3‰). We also examined additional models with smolts as a separate, one-species category. The model generates feasible combinations of dietary sources that satisfy isotopic mass balance, but does not create unique solutions (Phillips and Gregg 2003).

To assess the isotope mixing model, we modeled the annual muskellunge dietary requirements for the Saint John River (Table 1) using Fig. 3 of Bevelhimer et al. (1985) that predicts food intake (mass of individual) at varied water temperatures. We used seasonal water temperatures in the SJR (RAC, unpublished data). For individuals >4,000 g, we assumed they were mature, spawning, and therefore not feeding for a 2-week period in May when water temperatures were ~10°C (Scott and Crossman 1973). We next calculated the potential quantity of Atlantic salmon smolts that could be consumed and their dietary contribution based on an average smolt size of 40 g and out-migration period of 21 days in May and early June at the Mactaquac Dam (Jones et al. 2004; T. Goff, Fisheries and Oceans Canada, Mactaquac Biodiversity Centre, unpublished data). In these analyses, we calculated the maximum potential rates.

We used estimates of smolt out-migration for the SJR tributaries from Jones et al. (2004). All salmon reproduction is assumed to occur in the tributaries. The Tobique River out-migration is 3,600–9,500 smolts annually (average = 5,700/year) and Nashwaak River out-migrations averages 17,000 smolts/year (average = 8,500/year). There are four similar sized tributaries where Atlantic salmon may reproduce between Grand Falls, NB, and Fredericton, NB; therefore, the estimated total number of Atlantic salmon smolts that out-migrate past Fredericton is on the order of 60,000 (Table 1). Again, these estimates are maximum potential rates.

Table 1 The bioenergetics model of consumption of Atlantic salmon smolts by the muskellunge population downstream of Mactaquac Hydroelectricity Facility

Time period	Total days	Average °C[a]	g^{-1} g of muskellunge^{-1} day^{-1} [b]	Consumption per individual (of given size)		
				500 g	4,500 g	9,000 g
November–March	150	5	0.01	750	6,750	13,500
April	30	10	0.025	375	3,375	6,750
May	30	12.5	0.0375	562	2,531	5,063
June	30	15	0.05	750	6,750	13,500
July–September	90	25	0.125	5,625	50,625	101,250
October	30	15	0.05	750	6,750	13,500
Total yearly intake (g)				8,813	76,781	153,563
Diet during smolt migration period—last 2 weeks of May and first week of June (%)				5.3	3.9	3.9
Total # of 40 g smolts possibly consumed				12	74	148
Estimated annual diet of smolts (g) from isotope mixing model (average = 64%)				5,640	49,140	98,280
Estimated annual diet of smolts (#) from isotope mixing model				141.0	1,229	2,457
Estimates for a population of 100 muskellunge at base of dam (average size = 4,500 g)						
Estimated annual diet of smolts (#)—isotope mixing model				122,850		
Estimated annual diet of smolts (#)—bioenergetics model				7,383		
Estimate of # of smolts passing Mactaquac Dam[c]				~60,000		

[a] RAC, unpublished data

[b] from Bevelhimer et al. (1985)

[c] Jones et al. (2004)

Results

A total of 18 sub-adult to adult muskellunge were tracked over a 2-year period. They were not located on each tracking date, but the average number of dates when they were located was 15 ± 8. Total tracking periods averaged 293 ± 103 days. Their relative home ranges were 2.5–90.0 km and averaged 28.8 ± 25.2 km. The median and mode were 23 and 10 km, respectively.

Most muskellunge were located in the areas downstream of the Mactaquac Dam (Fig. 3). Nine individuals were trans-located upstream of the Mactaquac Dam and seven of these traveled back over or through the dam facility. The majority of muskellunge downstream of the dam exhibit skin lacerations and fin damage consistent with passage through a sluiceway turbine. Most were located in the islands along the east bank ~15 km from the dam during May when river temperatures were 5–10°C and Atlantic salmon smolts were passing through the reach (see Jones et al. 2004). Some remained and some dispersed upstream to the dam area and the main river channel by late May and into June. In winter, they preferred the slow, deeper reaches from the dam downstream to Fredericton.

Upstream of the dam, there were fewer fish to track (45 of our 268 total data points when fish were located = 17%), but these nine individuals traveled in proximity of the dam for short periods after being released and then either dispersed upstream to the Nackawic area (lacustrine) or upstream to Woodstock and Hartland (riverine) and seven eventually traveled downstream past the dam (Fig. 3). In winter, locations used upstream of the dam were lacustrine environments. One muskellunge, 89.5 cm fork length and 6,417 g wet weight (estimated age 5+; Stocek et al. 1999) traveled past the dam downstream to Fredericton after its release in the summer, and then up the Nashwaak River 26 km from the dam where it resided for the summer. Its ‘‘home pool’’ was 30 m long, 15 m wide, and <2 m deep.

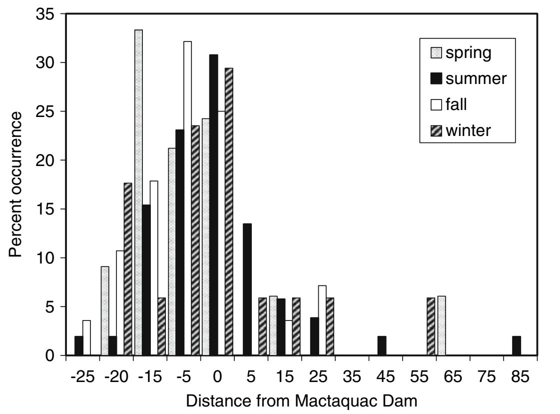

Fig. 3 Locations of radio-tagged muskellunge as % occurrence of tagged individuals in each of four seasons in the Saint John River, July 2000 to July 2003. Distances are from the Mactaquac Dam

Muskellunge captured at the base of the Mactaquac Dam had average δ^{13}C = –25.8 ± 1.7 and δ^{15}N = 13.9 ± 1.0 (n = 12). Values for other species and groups are given in Table 2. The values for the muskellunge adjusted for diet-tissue fractionation (0.4‰ for δ^{13}C, 3.4‰ for δ^{15}N; Post 2002) place them within the dietary source polygon for the categories modeled (Fig. 4).

According to the mixing model, stream fishes were the most important item in the diet of muskellunge, comprising 26–64% of the diet (Fig. 5). Forage fishes from the Mactaquac Dam were also important, comprising 2 to 48% (Fig. 5). All other groups were less important, with 0% contributions as the most feasible value (Fig. 5). When Atlantic salmon smolts were added separately as a dietary component, they were predicted to be an important item for muskellunge, comprising 38–80% of the diet.

The bioenergetics modeling of dietary requirements for muskellunge in the SJR downstream of the Mactaquac Dam suggests the total intake is 9–170 kg/annum for individuals ranging from 0.5 to 10.0 kg total body weight. For the 3-week period at the end of May and beginning of June (the period of muskellunge spawning and out-migration of Atlantic salmon smolts), total food intake ranged from 4 to 5% of the total annual intake for an individual muskellunge, which represents 12–164 Atlantic salmon smolts consumed if they were the only diet item (for 0.5–10.0 kg muskellunge, respectively). The isotope mixing model suggested the muskellunge diet ranged from 38 to 80% Atlantic salmon smolts. At 38% of a muskellunge's diet ranges from 33 kg or 84 smolts to 65 kg or 1,621 smolts if they were the entire diet (for 0.5 and 10.0 kg muskellunge, respectively). A smolt diet of 80% ranges from 71 kg or 176 smolts to 137 kg or 3,415 smolts (for 0.5 and 10.0 kg muskellunge, respectively). Assuming the average size for muskellunge downstream of the Mactaquac Dam in the Saint John River was 4.5 kg (average for tagged and isotope-sampled muskellunge), 100 individuals inhabit the reach (the most observed in a year was 58; Fig. 2), and only smolts were consumed, then the bioenergetics model predicts that 7,400 smolts would be consumed and the mixing model predicts 73,000–154,000 smolts would be consumed annually by the muskellunge downstream of the dam.

Table 2 Stable isotope levels for selected fishes captured at the base of the Mactaquac Dam, Saint John River, 1999 (average, 1 SD, and sample size)

Muskellunge		Atlantic salmon smolts		Forage fishes[a]		Smallmouth bass		Anadromous fishes[b]	
δ^{13}C	δ^{15}N	δ^{13}C	δ^{15}N	δ^{13}C	δ^{15}N	δ^{13}C	δ^{15}N	δ^{13}C	δ^{15}N
–25.8	13.9	–26.4	9.8	–25.6	11.5	–26.0	14.3	–19.1	12.6
1.7	1.0	1.9	0.9	1.7	0.8	0.8	1.4	1.2	0.9
12	12	19	19	97	97	21	21	71	71

[a] Forage fishes = *Alosa* spp. (young-of-the-year), brown bullhead, banded killifish (*Fundulus diaphanous*), creek chub (*Semotilus atromaculatus*), common shiner (*Luxilus cornutus*), golden shiner (*Notemigonus chrysoleucas*), lake chub (*Couesius plumbeus*), pumpkinseed sunfish (*Lepomis gibbosus*), white perch (*M. americana*), white sucker, and yellow perch

[b] Anadromous fishes = *Alosa* spp. (adults), sea lamprey, and striped bass

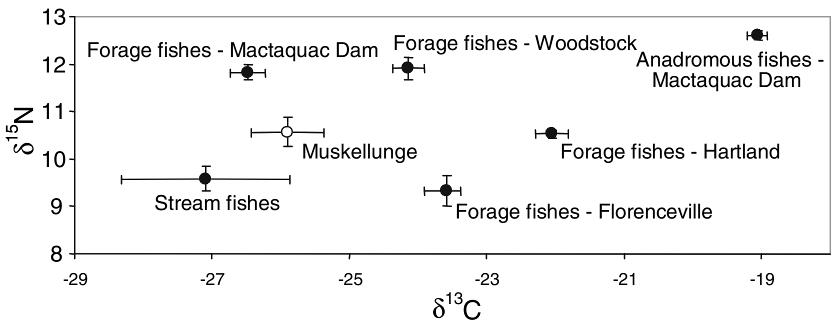

Fig. 4 δ^{15}N and δ^{13}C isotope values (average and 1 SE) for the fish community along the Saint John River and for a composite sample of stream fishes from New Brunswick rivers. Muskellunge values were adjusted by diet-tissue fractionation factors of 0.4‰ for δ^{13}C and 3.4‰ for δ^{15}N (Post 2002)

Discussion

Our tracking of muskellunge captured at the Mactaquac Dam indicates that there is a population of muskellunge in the middle reaches of the SJR from about Florenceville, NB, to Fredericton, NB. Large sub-adults and adults readily traveled up to 100 km upstream of the Mactaquac Dam in both lacustrine and river environments and passed over or through the dam. The apparent home ranges were variable in size extending from a few kilometers to 90+ km traveled along the river within a 2-year period, which is consistent with other populations (Strand 1986; LaPan et al. 1996). SJR muskellunge used a diversity of broad-scale habitats within their range, e.g., lacustrine, large river, and a small tributary. If they had a preferred habitat, it was not readily apparent; however, it would appear that a general, downstream movement by these large muskellunge was the trend given that 78% of individuals that were trans-located upstream of the dam made their way back downstream of the dam.

The muskellunge diet inferred from the stable isotope analyses suggests individuals have not been at the dam or in the downstream reaches for much of their lives. Rather, the isotope analyses support an origin upstream of Florenceville, or perhaps from one or more tributaries along the river. The difference in δ^{15}N and δ^{13}C between muskellunge and its reported principle forage of yellow perch and white sucker (Scott and Crossman 1973) for all sites along the main stem of the river was less than the 3.4‰ and 0.4‰, respectively, which is the typical difference between fish predators and their prey (Post 2002). Only the pooled stream fishes category appeared to align with muskellunge as an important dietary item. White muscle tissue reflects the amalgamated diet history of individual ectotherms over the longer-term of several years (Hesslein et al. 1993). If muskellunge in the middle and lower reaches arrive from upstream at age ≥ 2+, then they have already added a large proportion of their biomass in a more ^{15}N-depleted environment upstream (observed by Curry and Munkittrick 2005), i.e., their δ^{15}N should fit best in an upstream food web. Alternatively, reproduction and juvenile life history periods may occur within a tributary to the main stem because forested tributary environments also tend to be depleted in ^{15}N relative to larger, more developed main stems of rivers (Anderson and Cabana 2005). Atlantic salmon smolts are principally recruited from the tributary streams (Jones et al. 2004) and their average δ^{15}N = 9.8 ± 0.9‰ (from captures at the Mactaquac Dam). A top predator in their tributary streams is predicted to have δ^{15}N ~ 13.3‰ and the Mactaquac Dam muskellunge have an average δ^{15}N = 13.9 ± 1.0‰. There was no observational evidence suggesting muskellunge reproduce and juveniles rear in any of the middle and lower reach tributaries to the SJR, including no reports from the numerous anglers in these tributaries (one tracked muskellunge probably

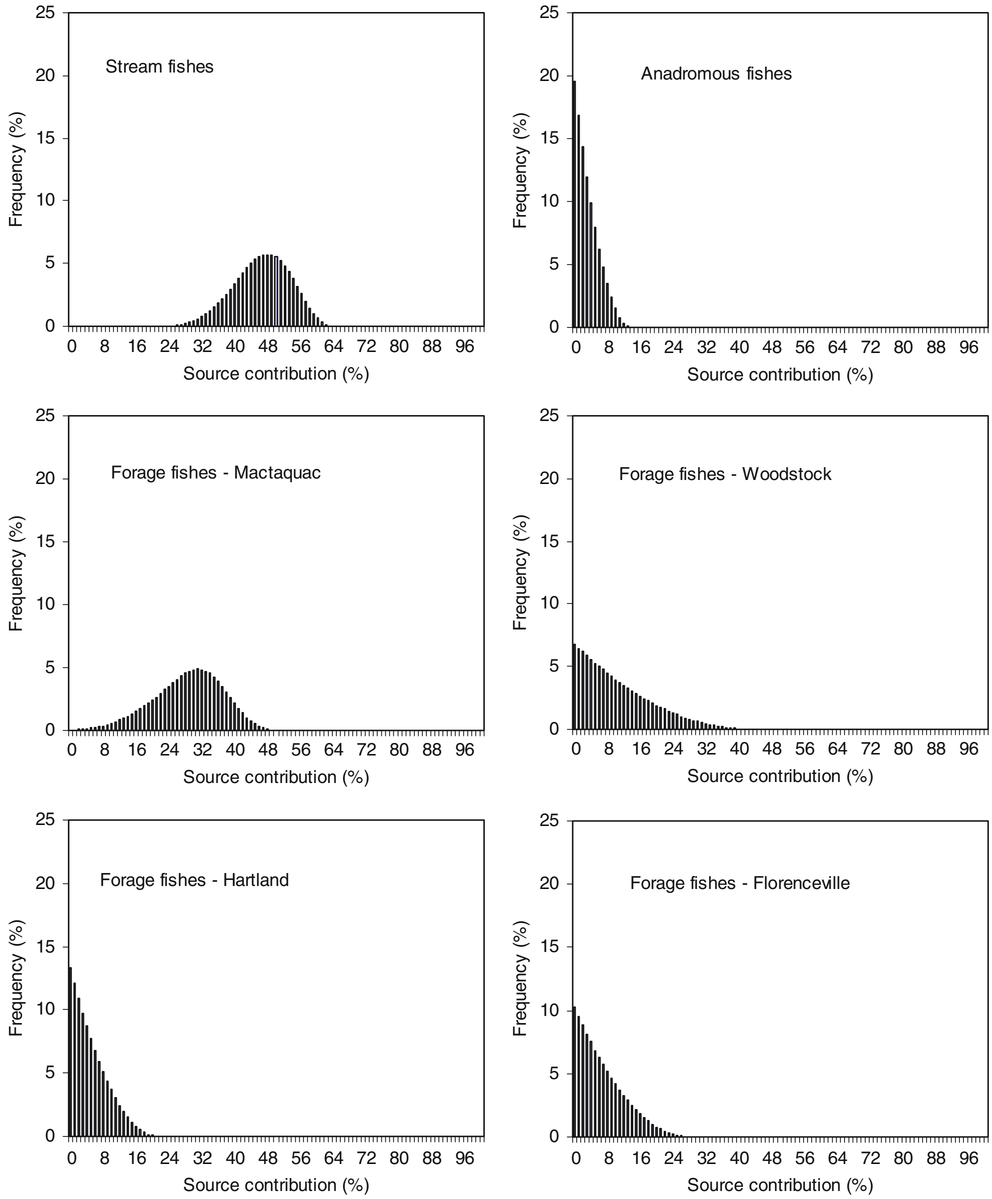

Fig. 5 Proportional estimates of feasible source contributions of various food items to the diet of muskellunge in the Saint John River estimated from a stable isotope mixing model

age 5+ moved into and resided in the Nashwaak River at Fredericton for a summer). Our evidence indicates there is a detachment between muskellunge and the food webs in the middle and lower reaches.

The disconnect causes problems for interpreting isotope analyses and resultant mixing models to predict muskellunge diet. The mixing model output suggested a large contribution to muskellunge diets by Atlantic salmon smolts (38–80%) or "stream fishes", with minor contributions from forage fishes and negligible contributions from anadromous fishes. Application of the bioenergetics models of Bevelhimer et al. (1985) contradicts the isotope mixing model for the smolt. The mixing model predicts smolt consumption could be 73,000–154,000, the bioenergetics models predict 7,400 smolts could be consumed, and total annual out-migration of smolts was estimated to be ~60,000. While the isotope mixing models suggest that muskellunge may be a major threat to Atlantic salmon populations in the river via consumption of smolts (but not grilse as the isotope signatures indicate), the smolt consumption estimate is quite doubtful.

Several factors in the isotope analysis must be considered as we attempt to revolve the complex interactions between muskellunge and their prey. First, mixing models are highly sensitive to diet-tissue fractionation for ^{13}C and ^{15}N (Connolly et al. 2005). In our analysis, we used mean values from the literature (0.4‰ for C, 3.4‰ for N—Post 2002); however, there was a large degree of uncertainty associated with those estimates, as fractionation is known to vary with nutritional state, age, etc. (McCutchan et al. 2003; Vanderklift and Ponsard 2003). We considered using fractionations for more narrowly defined species, but the literature contains no estimates of fractionation for species in the Esocidae family. Running the model using a lower fractionation estimate of 2.0‰ from McCutchan et al. (2003) returned similar dietary mixtures. Second, the isotopic signature of Atlantic salmon smolts was most similar to tributary food webs, which suggests and supports the hypothesis that muskellunge are recruited to the mainstem, either from upstream areas in general or tributaries. Finally, the abundance and biomass of Atlantic salmon smolts was extremely low relative to other potential prey for muskellunge in the system (Curry and Munkittrick 2005). Smolt availability for consumption is temporally limited to a brief pulse during their spring out-migration, which overlaps with muskellunge spawning. Availability is spatially limited because smolts move downstream rapidly and at night (Bakshtanskiy et al. 1980; Faangstam 1993) in the main channel of the river, while muskellunge are spawning in shallow, flooded, backwater areas (Scott and Crossman 1973; Dombeck 1986), e.g., the flooded islands upstream of Fredericton where they were located in spring, and feeding typically occurs in early morning and late evening at this time of year (Miller and Menzel 1986). Muskellunge most probably consumed some Atlantic salmon smolts as do esocids in other systems (Warner et al. 1968; Jepsen et al. 1998), but grilse or adult salmon have a low probability of being consumed based on the isotope signatures of anadromous fishes in the SJR. Many other fish predators that are significantly more abundant in the SJR (Curry and Munkittrick 2005) can consume smolts such as striped bass, *M. saxatilis* (Blackwell and Juanes 1998), smallmouth bass (Naughton et al. 2004), brown trout, *Salmo trutta* (Huntingford et al. 1988), and brook charr, *S. fontinalis* (Mohler et al. 2002). The best estimate of smolt consumption by muskellunge predicted a total of 7,400 smolts consumed downstream of the Mactaquac Dam if every muskellunge ate smolts only. Given these latter requirements, it is highly improbable that muskellunge have a significant effect on the salmon population in this reach of the SJR.

Since muskellunge began appearing at the Mactaquac Dam, only large sub-adults and adults have been captured. The number of captures has been increasing (although down in 2002 and 2003) and the population has grown to support a fishery and sport fishing association in the Woodstock, NB area (catch per unit effort = 0.8 muskellunge/angler-hour; C. Raynor, SJR Chapter, Muskies Canada, Inc., personal communication). Interestingly, all muskellunge recently captured in these reaches were larger individuals >3 kg. The smallest individual reported by the sport fishing association was 2.5 kg. Stocek et al. (1999) report two to five juveniles from the area and possibly one young-of-the-year from the islands at Fredericton (species identification was unconfirmed), but the majority were age 3+ and 4+ (63.8–93.4 cm total length, 1,850–6,275 g wet weight). We have conducted multiple fish surveys in the area from Florenceville to Fredericton, and specifically targeted juvenile esocids in the islands upstream of Fredericton where radio-tagged muskellunge were observed in spring during the time when spawning should have occurred; we have not yet located any juvenile muskellunge. Upstream of Grand Falls, NB, juveniles are regularly captured in fish community surveys and by local anglers (RAC, unpublished data; E. LeBlanc, personal communication). Given the absence of juveniles in the reach from Florenceville to Fredericton and the tendency for tracked individuals to move downstream, it may be that muskellunge are dispersing from reaches upstream of Florenceville where they are reproducing successfully, to the middle and downstream reaches. Our stable isotope results support this claim.

The complete effects of the introduced muskellunge in the SJR ecosystem will take time to resolve. Prior to the muskellunge's introduction, the chain pickerel, *E. niger* (1800s) and smallmouth bass (1940s) were introduced to the lower river (Livingstone 1951). These predators appear to have had no impact on Atlantic salmon in the river, which began to decline in population size in the 1980s. Regional fisheries managers have considered neither of these introduced predators be a significant factor in the management of Atlantic salmon. While the addition of another large predator suggests predation-risk will increase, it is important to understand that muskellunge numbers are low and their spatial and temporal habitats minimally overlap with Atlantic salmon. The greater challenge for managers and the river ecosystem will most probably be the muskellunge's longer-term, potential threats to native fishes and possible conflicts with the growing recreational fishery for muskellunge.

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