Marine feeding patterns of anadromous brook trout (*Salvelinus fontinalis*) inhabiting an estuarine river fjord[1]

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Abstract: This study describes the ontogenetic and seasonal feeding patterns of anadromous brook trout (*Salvelinus fontinalis*, also known as sea trout) inhabiting the estuarine Saguenay River (Quebec, Canada) using both stomach content and stable isotope analyses. Sea trout of the Ste. Marguerite River (Quebec, Canada) entered the saline waters of the Ste. Marguerite Bay in early May before venturing into the Saguenay River fjord for the remainder of the summer period. Upon their arrival, first-year migrants stayed relatively close to river mouths and initially fed on freshwater aquatic invertebrates. However, they quickly shifted their diet to marine prey items such as amphipods and mysids for the rest of their first summer at sea. These prey items were generally larger than freshwater prey; the prey spectrum at sea was both larger and wider than that found in freshwater and, as such, likely contributed to the trout's rapid growth rates at sea. The diet of migrants in subsequent years at sea (second-year migrants) consisted primarily of marine crustaceans and fish, the latter being most important when feeding in the upper Saguenay River. Trout shifted to piscivory at all marine sites at a size of 25 cm, regardless of time spent at sea, although the importance of piscivory varied with season and site.

Résumé : Notre étude décrit les patrons ontogéniques et saisonniers d'alimentation de l'omble de fontaine anadrome (« truite de mer »; *Salvelinus fontinalis*) qui habite l'estuaire du Saguenay (Québec, Canada) à l'aide à fois de l'étude des contenus stomacaux et de l'analyse des isotopes stables. La truite de mer de la rivière Sainte-Marguerite (Québec, Canada) pénètre dans les eaux salines de la baie de Sainte-Marguerite au début de mai avant de s'aventurer dans le fjord du Saguenay pour y passer le reste de l'été. À leur arrivée, les migrateurs d'un an restent relativement près des embouchures des rivières et se nourrissent au départ d'invertébrés aquatiques d'eau douce. Ils changent cependant rapidement de régime et utilisent des proies marines telles que des amphipodes et des mysidacés pour le reste de leur premier été en mer. Ces proies sont généralement de plus grande taille que les proies d'eau douce; la gamme de proies en mer est aussi plus importante et plus étendue que celle d'eau douce et elle contribue ainsi aux taux élevés de croissance de la truite en mer. Le régime alimentaire des migrateurs des années subséquentes en mer (les migrateurs de seconde année) comprend surtout des crustacés et des poissons marins, ces derniers étant particulièrement importants lorsque la truite de mer se nourrit dans le Saguenay supérieur. Dans tous les sites marins, la truite de mer devient ichtyophage à une taille de 25 cm, quel que soit le temps passé en mer, bien que l'importance de l'ichtyophagie varie en fonction de la saison et du site.

[Traduit par la Rédaction]

Introduction

In many populations of salmonids that access the sea, migrant and resident individuals of the same population coexist as juveniles, with the former spending a portion of their life cycle feeding in saline waters and the latter completing their entire life cycle in freshwater. Those that migrate from freshwater to the sea, returning as large adults to freshwater for spawning, follow an anadromous life cycle. Anadromous brook trout (*Salvelinus fontinalis*, also known as sea trout) naturally occur in northeastern North America in river systems that are open to the sea (Smith and Saunders 1958; Dutil and Power 1980; Castonguay et al. 1982). They generally experience a short but seasonally determined sea residence, returning to freshwater for winter (Dutil and Power 1980; Power 1980), a response most likely necessitated by

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their inability to osmoregulate in cold waters (Saunders et al. 1975). In recent years, angling pressure on sea trout has escalated as returns of Atlantic salmon (*Salmo salar*) to rivers have declined. Unfortunately, few studies involving the anadromous phase of the life cycle have been conducted, limiting our understanding and, thus, ability to implement sustainable management practices.

Juvenile sea trout, before their first seaward migration, exhibit high consumption rates but low growth efficiencies (ratio of growth to consumption) in freshwater compared with residents, the consequence of higher metabolic costs (Morinville and Rasmussen 2003, 2006). The finding that sea trout (migrant) obtain more food in freshwater compared with residents before migration and still migrate suggests that they do not receive enough energy to satisfy their high energetic demands. Juvenile sea trout may thus experience growth bottlenecks sooner than residents, leading them to change habitats in search of an efficient food supply (low cost of capture but high energetic gain). Accordingly, anadromous fish do grow faster in the sea than their resident counterparts of the same age class (Castonguay et al. 1982; Lenormand et al. 2004), suggesting reduced activity costs (swimming, foraging, and other behavioural activities) and (or) better feeding opportunities at sea. Such feeding opportunities may be in the form of differences in overall productivity or differences in the availability of optimally sized prey (Keeley and Grant 2001). Marine systems are generally thought to be more productive for fish than freshwater systems, based on the migratory tendencies of salmonids in north-temperate latitudes (Gross et al. 1988).

In general, fish need to eat large prey to sustain growth and attain large sizes. Foraging costs, both in terms of the time spent actively searching and the number of feeding attempts, increase as prey sizes become small in relation to the size of the predator (Kerr 1971; Kerr and Ryder 1977). Optimal growth returns can thus be easily achieved when the diet is mostly composed of large prey (Kerr 1971; Wañkowski and Thorpe 1979; Sherwood et al. 2002). As such, fish, including salmonids, tend to eat larger prey with increasing size, displaying ontogenetic diet shifts from planktivory to benthivory and ultimately to piscivory (Werner and Gilliam 1984; Mittelbach and Persson 1998; Keeley and Grant 2001). Salmonids tend to eat large prey (fish) sooner in ocean habitats than when inhabiting streams, allowing individuals to attain large sizes more quickly (Keeley and Grant 2001).

Brook trout are commonly considered to be opportunistic feeders, their diet changing with size, season, and habitat (Power 1980). However, few studies report in detail the diet of the anadromous form. Of those that exist, most provide only general descriptions of prey items found in stomachs. These studies commonly report in the diet the presence of amphipods, mysids, and fish, including sand lance (*Ammodytes* sp.), sticklebacks (*Gasterosteus*), smelt (*Osmerus* sp.), and hake (*Urophycis* sp.) (Wilder 1952; Dutil and Power 1980; O'Connell 1982). Only one study has acknowledged the importance of the effect of ontogeny or season on diet of brook trout (Gaudreault et al. 1982), and no study has attempted to directly link diet to the movement patterns at sea. Such information is necessary for implementing sustainable management plans for sea trout, and thus a better understanding of seasonal diet requirements across marine habitats is necessary to, for example, protect the most important feeding grounds.

Lenormand et al. (2004) recently described the ontogenetic and seasonal movement patterns of sea trout migrating to the estuarine Saguenay River (SR) from the Ste. Marguerite River (SMR) in Quebec, Canada. Sea trout of the SMR migrate in May, as early as age 1+, initially entering the saline waters of the SR by passing through the estuarine Ste. Marguerite Bay (SMB), where they remain for a few weeks acclimatizing to the salinities and temperatures of the new habitat, staying relatively close to freshwater inputs (Lenormand et al. 2004). As summer progresses and water temperatures increase, trout gradually migrate out from the bay, with the largest trout leaving sooner to enter the deeper, colder, more saline waters of the Saguenay fjord (SR fjord) (Lenormand et al. 2004). Unlike most anadromous brook trout populations that seem to remain close to the influence of their natal river (White 1940; Dutil and Power 1980), anadromous populations of the SR fjord are unique in that they migrate large distances, upwards of 100 km, experiencing relatively low salinities and high temperatures across the estuary (Chassé and Côté 1991; Lenormand et al. 2004).

The present study investigates the diet of anadromous brook trout immediately upon entering the sea through an estuarine bay. The main objectives of this study were (*i*) to compare the food availability (feeding opportunities) between freshwater and the initial site of sea entry and (*ii*) to describe the feeding patterns of anadromous brook trout during both their first year at sea (hereafter referred as first-year migrants) and their second year or more at sea (hereafter referred as second-year migrants) to better understand the growth patterns experienced at sea. We predicted that the initial site of sea entry, the estuarine SMB, would have more food available than found in freshwater, either in total invertebrate biomass and (or) mean invertebrate size, including a larger range of prey sizes. Seasonal feeding patterns of anadromous brook trout (sea trout) were described across sites in the SR, including the monthly detailed diet of first-year migrants captured in the SMB using stomach content and stable isotope analyses. We expected that sea trout would initially feed on freshwater-derived prey upon sea entry but that they would quickly shift to larger marine-derived prey sources, leading to rapid growth. We also expected that tissues of first-year migrants would become enriched in stable carbon signatures ($\delta^{13}C$) over time because of the enriched $\delta^{13}C$ values of marine prey items compared with those of freshwater (Fry and Sherr 1984). Trout were also predicted to shift to higher trophic levels over time, as indicated by enriched muscle tissue $\delta^{15}N$ signatures.

Materials and methods

Study site

This study was conducted in the SMR system and in the estuarine SR (Quebec, Canada; 48°27′N, 69°95′W; Fig. 1). The SMR flows into the estuarine SR 25 km upstream from the St. Lawrence River maritime estuary (Quebec, Canada). The SMR is home to the largest anadromous brook trout population of the Saguenay River basin (Lesueur 1993). Anadromous brook trout migrate from mid-May to early

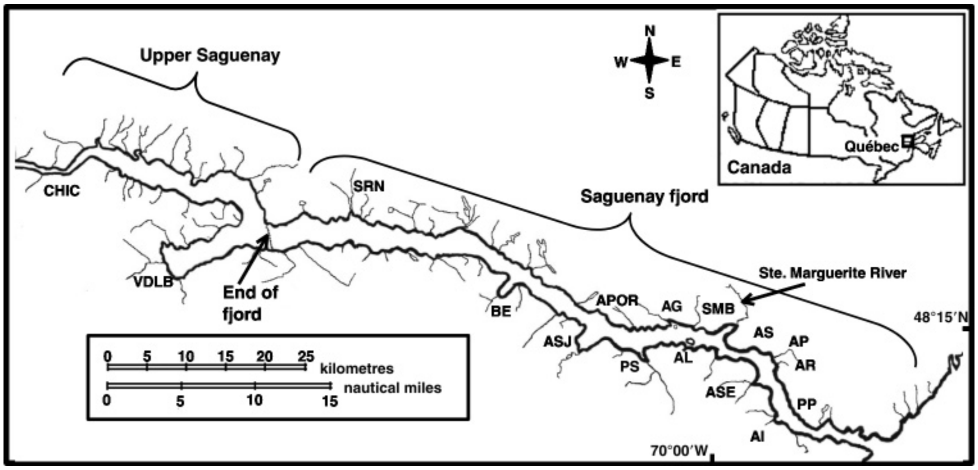


Fig. 1. Map of Saguenay River (Quebec, Canada) sampling sites located in the Saguenay fjord and the upper Saguenay, separated by "End of fjord". Abbreviations: CHIC, Chicoutimi (now City of Saguenay); VDLB, Ville-de-la-Baie (now City of Saguenay); SRN, Ste-Rose-du-Nord; BE, Ste. Eternité Bay; ASJ, Anse St-Jean; APOR, Anse-du-Portage; SMB, Ste. Marguerite Bay; ASE, Anse-St-Étienne; AS, Anse-de-Sable; AP, Anse-à-Pierre; AR, Anse-de-Roche; PP, Pointe à Passe-Pierre; AI, Anse-aux-Petites-Îles; AG, Anse-à-Gagnon; AL, Anse-à-l'Île.

June, as early as age 1+, initially passing through the large, shallow SMB before venturing into the SR (Thériault and Dodson 2003; Lenormand et al. 2004). The SR is divided into two main sections: (*i*) the Saguenay fjord, defined as the last downstream 100 km of the SR under tidal influence and characterized by a mixing zone between freshwater upstream sources and salt-water inputs from the St. Lawrence River maritime estuary, and (*ii*) the upper SR portion. Freshwater inputs into this subarctic fjord are quite variable, with a strong thermohaline stratification occurring between May and October (Chassé and Côté (1991) and references therein; Lenormand et al. 2004). During this period, the water column is divided into a thin, mixed layer (5–10 m) of warm (5–15 °C), brackish (0–18 PSU (practical salinity units)) water and a thick (up to 275 m), underlying layer of cold, saline water (<0.5 °C, >26 PSU at 15 m). The thermohaline stratification regresses in the fall as exchanges between the two layers increase and salinity at the surface rises with decreasing surface temperatures. The ice-cover period occurring between December and April is characterized by surface temperatures around 0 °C and salinity around 7 PSU at the surface. Increasing inputs of freshwater and surface water temperatures during the ice-melt period (mid-March to early May) re-establishes the stratified water column.

Food availability at sea entry

Food availability for both May and August 1998 was compared between freshwater sites located in three tributaries of the SMR (Morin, Allaire, and Épinette; for location of streams, see Lenormand 2003) and 6–7 randomly selected sites located along 30 km of the SMR and multiple randomly selected marine sampling locations (~20 sites) in the SMB, the initial site of sea entry. Sampling was conducted using 1.0 mm mesh kicknets. Sampling in the SMB occurred at tide edges both at high and low tides, depending on location. Some sites were only accessible at low tide. In flowing-water sites (river, stream, and some bay sites), rocks were kicked around in an area corresponding to the width (0.45 m) of the kicknet squared (0.20 m^2) for approximately 30 s, displacing any invertebrates into the kicknet. An average of 10 samples were taken at each site, and all captured invertebrates were pooled for subsequent estimates. In marine sites with no current, the kicker displaced rocks and moved the kicknet in a circle with a radius equivalent to the width of the kicknet (0.64 m^2). This created current and allowed invertebrates to be captured in the kicknet. The same kicker (G.R. Morinville) performed all samplings. All samples were placed in bags and frozen for subsequent taxonomic analyses.

All invertebrates were sorted according to their taxonomic group to the level of order and were counted. Individuals from each taxon were pooled according to their size (size classes in millimetres) when applicable, as determined from the modes of taxon-specific length-frequency distributions. Lengths to the nearest 1 mm were taken using a ruler. This allowed for a more detailed description of the relative contribution of each size class to all classes of a specific taxon for all sites. The relative contribution of each size class was then averaged over all marine and freshwater-specific sites. For the sake of simplicity, only the common taxonomic groups found in the diet of brook trout inhabiting freshwater (mayfly, caddisfly, and stonefly) or the sea (amphipod and mysid) where multiple size classes existed were considered.

Wet weights were measured after the removal of excess moisture with absorptive tissue, and dry weights of samples were taken after samples had dried for 48 h at 60 °C in a drying oven. Food availability was estimated by measuring the mean biomass of pooled invertebrates from each sampling site, expressed as the amount of dry weight of invertebrate prey in grams of dry weight per square metre ($g\ dw \cdot m^{-2}$; Boisclair and Leggett 1985) and was compared between freshwater and marine sites using both. Mean invertebrate size ($mg\ dw \cdot individual^{-1}$) was also estimated and compared between freshwater and marine sites by pooling the dry weights of all invertebrates within a sample (site) and dividing this value by the total number of individuals in that sample. All comparisons between freshwater and marine sites for mean biomass and mean invertebrate size were performed using *t* tests.

Ontogenetic and seasonal feeding patterns

A dual approach using both stomach content analysis (SCA) and stable isotope analysis (SIA) was employed to describe the feeding patterns of anadromous brook trout inhabiting the SR.

Fish collection

Fish stomachs were obtained from trout captured by anglers, from trout obtained for a parallel study (Lenormand 2003; Lenormand et al. 2004), and from additional sampling throughout the SMR, SMB, and multiple SR sites (Fig. 1). At the time of the study, fishing for anadromous brook trout was permitted in the SR, including the SMB, all year round and in the SMR from mid-June to the end of October, allowing for samples from anglers across seasons and sites. Stomachs obtained from anglers throughout the years 1998 to 2001 were available because of a parallel mark–recapture program occurring in the SMR and SMB. Anglers received compensation when they returned tagged fish (Lenormand et al. 2004). Stomachs obtained from trout captured in the SMR during the winter were also made available through this parallel study (Lenormand et al. 2004). Stomachs were either analyzed the day of capture or frozen for future analysis. Both the fork length (to the nearest millimetre) and weight (to the nearest 0.01 g) of sampled trout were measured, although in some cases, this was not possible for trout captured by anglers.

Trout were also sampled in 2000 to 2002 at the onset of sea entry in the SMB in May and every 2–4 weeks thereafter until October using a 40 m beach seine (0.5 cm mesh, 1.5 m deep). In certain years, it was more difficult to catch trout during July and August in the SMB because trout tend to leave the SMB for more saline, colder, deeper areas of the SR with increasing temperatures (Lenormand et al. 2004). Sampling in July and early August was conducted in Anse-de-Sable (AS) and Anse-à-Pierre (AP) (Fig. 1). Approximately 20 trout ranging in size were sacrificed at each sampling interval. Both stomach contents and muscle tissue biopsies (for stable isotopes) were obtained from trout for subsequent diet analyses.

Stomach content analysis (SCA)

The percentage of empty stomachs (%ES) was estimated and used as a measure of feeding activity. Non-empty stomachs consisted of predominantly whole undigested prey items with the exception of freshwater aquatic invertebrate larvae that were sometimes partially digested. Prey items were identified to order or genus for both freshwater aquatic invertebrate and marine prey. Excess moisture was removed from prey items, and like items from each stomach were weighed to the nearest 1 mg (wet weight).

In SR sites (including SMB, upper SR, and Saguenay fjord sites), prey items were subsequently assigned to 10 prey categories: freshwater aquatic larvae, terrestrial insects excluding beetle (coleopteran), beetle, amphipods (mostly *Gammarus* sp.), striped *Gammarus* (*Gammarus tigrinus*), polychaete, mysid, panaeid shrimp, fish, and "other", which includes unidentified prey, plant matter, winged insects including newly emerged flies, and miscellaneous prey items. In the SMR, prey items were assigned to nine prey categories: freshwater aquatic larvae, terrestrial insects excluding beetle, beetle, small mammal, salmonid eggs, winged insects including newly emerged flies, plant matter, fish, and "other", which includes all unidentified prey.

Two stomach content analysis methods were applied to describe the diet composition of anadromous brook trout (Hyslop 1980). The estimates were generated using only the trout having non-empty stomachs. The relative importance of individual prey types was assessed in terms of percentage of occurrence (%*O*) and percentage by weight (%*W*), where the total wet weight of each prey category was expressed as a percentage of the overall weight of stomach contents, termed "prey wet weight contribution" (Clark 1985). %*W* is presented for all prey items in figures, whereas for %*O*, only the two most dominant prey items in fish stomachs are presented in tables.

To describe the ontogenetic and seasonal marine feeding patterns of brook trout, samples were first grouped according to trout type, either first-year migrants (trout in their first year at sea) or second-year migrants (trout in their second or more years at sea). For trout captured in the SMB, stomach contents were pooled by month for years 1998 to 2002, because large samples were available. Monthly means for %ES, %*O*, and %*W* were subsequently generated using pooled years. In contrast, because of limited available captures of brook trout in the SR for any given year and at any given site, monthly %ES, %*O*, and %*W* estimates were obtained by pooling all stomach contents obtained across years at a given site for a given month. These site-specific monthly estimates were further pooled according to their location of capture in the SR, either Saguenay fjord sites or upper SR sites, generating mean monthly estimates. Stomachs obtained from trout captured in the SMR were first pooled by month for years 1998 to 2000, and monthly means for %ES, %*O*, and %*W* were calculated using pooled years.

Stable isotope analysis (SIA)

Carbon and nitrogen stable isotopes ($\delta^{13}C$ and $\delta^{15}N$, respectively) were used to describe the long-term feeding patterns of first-year migrant brook trout from their arrival at sea into the SMB and throughout the summer in relation to the SMB food web. Muscle biopsies were taken from first-year migrant trout captured in the SMB in years 2000 to 2002. Changes in both $\delta^{13}C$ and $\delta^{15}N$ were followed according to the size of migrants and time of capture. The muscle tissue of resident brook trout captured in a tributary of the SMR (Morin Stream) during June and July 1999 were also analysed for stable isotopes, which allowed comparisons between the different regressions with those of sea trout using analyses of covariance (ANCOVA).

To describe the food web leading to sea trout, all potential invertebrate prey items found in the SMB and neighbouring sites downstream to the SMB, including Anse-de-Sable and Anse-à-Pierre, during the years of study were analysed for stable isotopes. Invertebrate prey items, collected using a kicknet, included amphipods (*Gammarus* sp. and *Gammarus tigrinus*), polychaetes, mysids, and freshwater aquatic larvae. Panaeid shrimp were also analysed and captured during seine

Fig. 2. Mean invertebrate biomass (g dry weight (dw)·m^{-2}) for sites located in the Ste. Marguerite River and Ste. Marguerite Bay in (*a*) May and (*b*) August. No significant differences in invertebrate biomass were found between river and bay sites in either May (t = –0.89, df = 25, p = 0.38) or August (t = –0.22, df = 25, p = 0.83). Broken lines and adjacent numbers indicate mean biomass estimates.

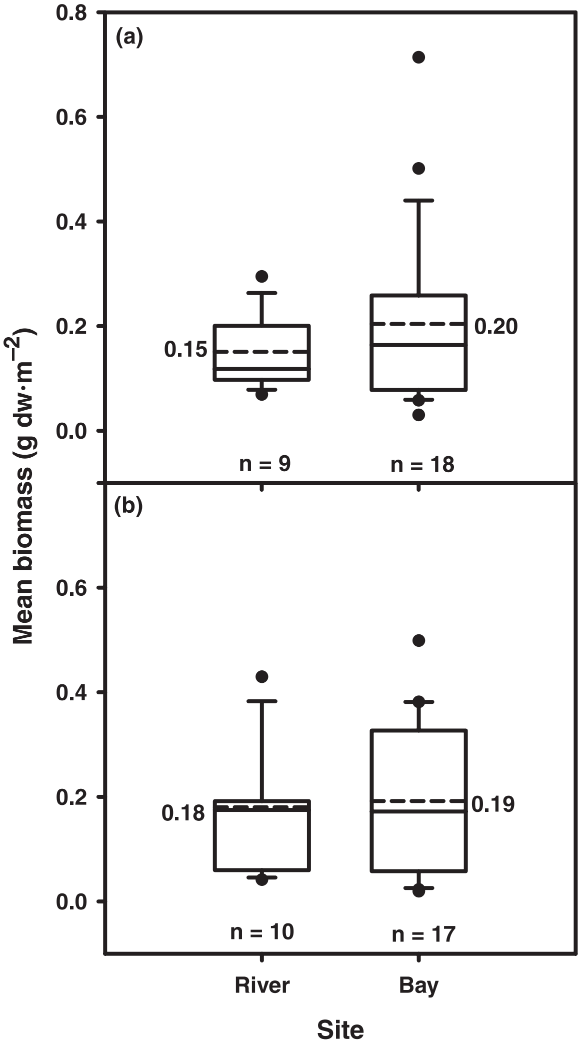
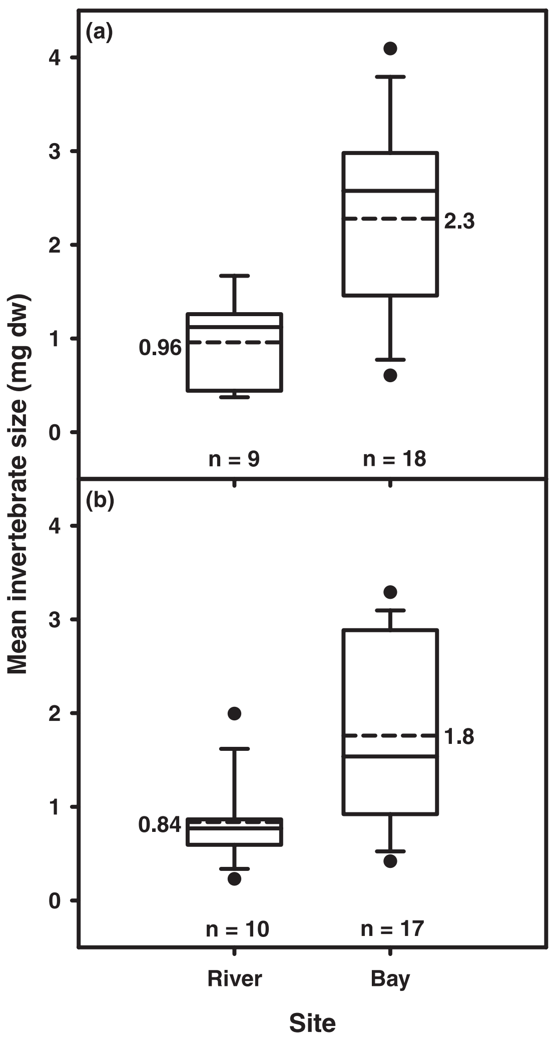


Fig. 3. Mean invertebrate size (mg dry weight (dw)·individual^{-1}) for sites located in the Ste. Marguerite River and Ste. Marguerite Bay in (*a*) May and (*b*) August. River sites had smaller invertebrates than bay sites in both May (t = –3.5, df = 28, p = 0.001; U = 28.0, p = 0.003) and August (t = –2.7, df = 25, p = 0.013; U = 34.0, p = 0.010). Broken lines and adjacent numbers indicate mean sizes.



hauls targeting trout. Fish including threespine sticklebacks (*Gasterosteus aculeatus*) and banded killifish (*Fundulus diaphanus*) were sampled using minnow traps baited with white bread. In addition, muscle biopsies were taken from larger prey fish, including smelt and sand lance, found in the stomachs of certain trout.

Stable carbon and nitrogen isotope analyses were performed using a continuous-flow Finnigan MAT Delta plus mass spectrometer (Finnigan MAT GmbH, ThermoQuest Corp., Barkhausenstr. 2, 28197 Bremen, Germany; G.G. Hatch Isotope Laboratory, University of Ottawa, Ottawa, Ontario, Canada). Stable isotope ratios are normally expressed in delta (δ) notation, defined as the parts per thousand (‰) deviation from a standard material: $\delta^{13}C$ or $\delta^{15}N$ = $[(R_{\text{sample}}/R_{\text{standard}}) - 1] \times 1000$, where R = $^{13}C/^{12}C$ or $^{15}N/^{14}N$. The standard material is Pee Dee belemnite (PDB) limestone for $\delta^{13}C$ and atmospheric nitrogen for $\delta^{15}N$.

Results

Food availability at sea entry

No significant differences were found between river and stream sites for either mean invertebrate biomass estimates or mean invertebrate sizes in either May or August 1998. River and tributaries were thus pooled for all subsequent analyses.

Mean biomass estimates in May 1998 ranged from 0.069 to 0.30 g dw·m^{-2} and from 0.030 to 0.71g dw·m^{-2} for river and bay sites, respectively (Fig. 2). In August, biomass ranged from 0.041 to 0.43 g dw·m^{-2} and from 0.020 to 0.50 g dw·m^{-2} for river and bay sites, respectively. No significant differences in mean biomass were found between river and

Table 1. Mean contribution (percent of total) of each size class to all size classes of invertebrate taxa obtained during kicknet sampling in freshwater (river) and marine sites (bay) in May and August 1998 for commonly reported prey types found in the diet of brook trout (*Salvelinus fontinalis*).

				May		August	
Site	Invertebrate	Size class	Size-class range (mm)	Numbers[a]	Percent of total[b]	Numbers[a]	Percent of total
River	Mayfly	S	0–4	1106	**56**	734	**70**
		M	5–10	815	42	304	30
		L	>10	18	2	0	<1
	Caddisfly	S	0–8	237	**54**	1215	**56**
		M	9–15	131	44	929	43
		L	>15	12	2	22	1
	Stonefly	S	<10	406	**68**	161	**87**
		M	10–20	174	26	22	6
		L	>20	24	6	7	7
Bay	Amphipod	S	0–5	889	29	1229	27
		M	6–9	1856	**46**	3391	**61**
		L	10–15	921	22	252	11
		XL	16–20	75	2	25	1
		XXL	>20	48	1	3	<1
	Striped Amphipod	S	0–5	92	7	1189	25
		M	6–9	746	37	601	**61**
		L	10–15	1130	**55**	168	13
		XL	16–20	26	1	1	1
		XXL	>20	1	<1	0	<1
	Mysid	S	0–10	895	**83**	49	8
		M	11–20	14	17	3534	**91**
		L	>20	69	0	38	1

Note: S, M, L, XL, and XXL refers to small, medium, large, extra large, and extra extra large, respectively. The size class with the highest overall mean contribution for each invertebrate is bolded.

[a] Numbers shown here do not take into account the density of invertebrates at each site.

[b] Percent of total is the mean contribution of each size class to all classes at each site and averaged over all sites.

bay sites in either May ($t = -0.89$, df = 25, $p = 0.38$) or August ($t = -0.22$, df = 25, $p = 0.83$).

In May 1998, mean invertebrate size ranged from 0.36 to 1.9 mg dw and from 0.60 to 4.2 mg dw for river and bay sites, respectively (Fig. 3). Invertebrate sizes varied in August between 0.23 and 2.0 mg and between 0.40 and 3.4 mg for river and bay sites, respectively. Invertebrates from river sites were smaller on average than those from bay sites for both May ($t = -3.5$, df = 28, $p = 0.001$) and August ($t = -2.7$, df = 25, $p = 0.013$).

Length-frequency distributions (data not shown) of sorted invertebrate taxonomic groups from freshwater sites revealed three size classes (small, S; medium, M; and large, L), ranging in size from 0 to >20 mm in length, for mayfly, caddisfly, and stonefly (Table 1). Across all freshwater taxa, invertebrates comprised mostly the smallest size category (S), ranging from 54% (caddisfly) to 68% (stonefly).

In contrast, five size categories (S; M; L; XL, extra large; and XXL, extra extra large), ranging in size from 0 to > 20 mm, were found for amphipods inhabiting the SMB. A greater number of amphipods were categorized as being medium- or large-sized, evident in both May and August. For mysids, most individuals were small during the month of May; however, by August, medium-sized individuals dominated the size spectrum.

Ontogenetic and seasonal feeding patterns

Stomach content analysis (SCA)

Ste. Marguerite Bay

In the SMB, a total of 972 and 492 stomachs of first- and second-year migrants, respectively, were analysed (Table 2). The mean %ES across months ranged from 8.8% to 20.1% for first-year migrants and from 14.7% to 76.2% for second-year migrants. This amounted to a total of 808 first-year migrants with non-empty stomachs captured between May and October, ranging in size from 114 to 231 mm (Table 3). Second-year migrants with non-empty stomachs (total n = 363) were larger, ranging in size from 220 to 337 mm.

Freshwater aquatic invertebrate larvae and polychaetes contributed the most to the overall wet weight of stomach contents in May, which agrees with the two most common prey items found in first-year migrant stomachs (Fig. 4; Table 4). From June to October, over 50% of the overall wet weight of stomachs consisted of amphipods (*Gammarus* sp.), the most common prey item found in stomachs. In July, terrestrial insects made up an important proportion of the diet, totalling almost 40% of contents. In addition to amphipods, mysids and polychaetes also contributed relatively highly to the diet of first-year migrants from August to October. Prey fish contributed only minimally to the overall weight of the

Table 2. Number of analysed stomachs (*N*) and percentage of empty stomachs (%ES; ±1 standard error) from first- and second-year migrant brook trout (*Salvelinus fontinalis*) captured in Ste. Marguerite Bay (SMB), the upper Saguenay River (upper) and Saguenay fjord (fjord), and Ste. Marguerite River (SMR) in years 1998 to 2002.

	First-year migrants			Second-year migrants		
Month	Site	*N*	%ES	Site	*N*	%ES
March–May	—	—	—	Upper	17	15.2 (8.8)
April	—	—	—	SMB	5	40
May	SMB	153	13.4 (4.6)	SMB	263	19.1 (2.5)
	—	—	—	Fjord	14	5.0 (5.0)
June	SMB	235	20.1 (6.2)	SMB	106	14.7 (8.0)
	Fjord	14	4.2 (2.9)	Fjord	57	22.9 (15.5)
June–July	Upper	—	—	Upper	5	12.5 (12.5)
July	SMB	72	18.4 (8.5)	SMB	27	15.9 (8.3)
	Fjord	66	9.8 (6.1)	Fjord	32	8.3 (5.3)
August	SMB	60	8.8 (2.5)	SMB	19	39.2 (14.2)
	Fjord	53	22.1 (19.4)	Fjord	13	11.1 (11.1)
September	SMB	283	20.1 (5.8)	SMB	54	38.7 (9.8)
	Fjord	18	6.7 (6.7)	Fjord	6	16.7 (16.7)
	SMR	170	44.7 (10.3)	SMR	204	55.0 (4.2)
October	SMB	169	15.0 (7.8)	SMB	5	20
October–November	Upper	11	46.5 (3.6)	—	—	—
October	SMR	209	56.7 (9.6)	SMR	212	48.6 (2.9)
November	—	—	—	Upper	4	50
December–February	Upper	19	19.4 (10.0)	Upper	18	26.9 (10.9)
January–February	—	—	—	SMB	13	76.2 (9.6)
February	—	—	—	SMR	10	90

contents (less than 5%) and were found in only a fraction of stomachs (5%). Mysids were often found in first-year migrant stomachs, although their contribution to the overall weight of the stomachs was minimal. Most piscivorous individuals exceeded 25 cm in length (Fig. 5). Overall, amphipods consistently contributed the most to the diet of first-year migrants in the SMB across months following the month of May.

As seen for first-year migrants in May, freshwater invertebrate larvae and polychaetes contributed the most to the overall wet weight of stomach contents from second-year migrants, corresponding to the two most dominant prey items occurring in the diet (Fig. 4; Table 4). In June, the diet of second-year migrants was comprised mostly of amphipods (40%) and polychaetes (20%). Contrary to the diet of first-year migrants, fish (all species combined, including sticklebacks, banded killifish, sand lance, and smelt) constituted a large portion of the diet of second-year migrants, but these were mostly found in trout larger than 25 cm (Fig. 5), with %*W* estimates ranging from 17% to 33%. The contribution of amphipods to the diet remained relatively high from July to September, with %*W* estimates ranging from 23% to 59%. Mysids contributed mostly to the diet of second-year migrants in the month of September, with a %*W* of almost 30%. Panaied shrimp occurred frequently in the diet; however, their %*W* was relatively low in comparison with the other prey items.

Saguenay River

Brook trout samples were obtained throughout the Saguenay River, including sites located in the fjord and its upper section. A total of 181 and 166 stomachs of first- and second-year migrants, respectively, were analysed across sites and years (Table 2). Of these, 4.2% to 46.5% of first-year migrants were empty, whereas 5.0% to 50% of second-year migrants were empty. As observed in the SMB, the %ES of both first- and second-year migrants was low during the summer months. Of the trout with non-empty stomachs, 160 were first-year migrants, with mean sizes ranging from 135 to 273 mm (Table 5). Second-year migrants (n = 138) were larger, with mean sizes ranging from 254 to 481 mm.

Amphipods were clearly the most dominant prey item of first-year migrants captured in the Saguenay fjord, in terms of both %*W* (ranging from 50% to 70%) and %*O* (ranging from 54% to 75%) between June and September (Fig. 6; Table 6). Only in June did terrestrial insects contribute strongly to the diet of first-year migrants, comprising 36% of the total wet weight of contents. In contrast, freshwater aquatic invertebrates, terrestrial insects, and fish contributed most to the diet of trout captured in the upper Saguenay sections in November. In winter, prey fish became the dominant item, comprising over 75% of total wet weight. As observed for the SMB, prey fish were mostly found in stomachs of trout larger than 25 cm (Fig. 5).

In the fjord, amphipods and fish contributed the most to the overall wet weight of contents across months, ranging from 26% to 50% and from 16% to 65%, respectively, for second-year migrants (Fig. 6). Terrestrial insects occurred frequently in stomachs, although their overall wet weight contribution was low (Table 6). In August, mysids contributed 34% of the overall wet weight of contents. In contrast, prey fish clearly contributed the most to the overall weight of stomach contents of second-year migrants captured in the

Table 3. Sample size (*N*) and mean size (±1 standard deviation) of first- and second-year brook trout (*Salvelinus fontinalis*) migrants captured in the Ste. Marguerite Bay (SMB) in May to October in years 1998 to 2002 with non-empty stomachs.

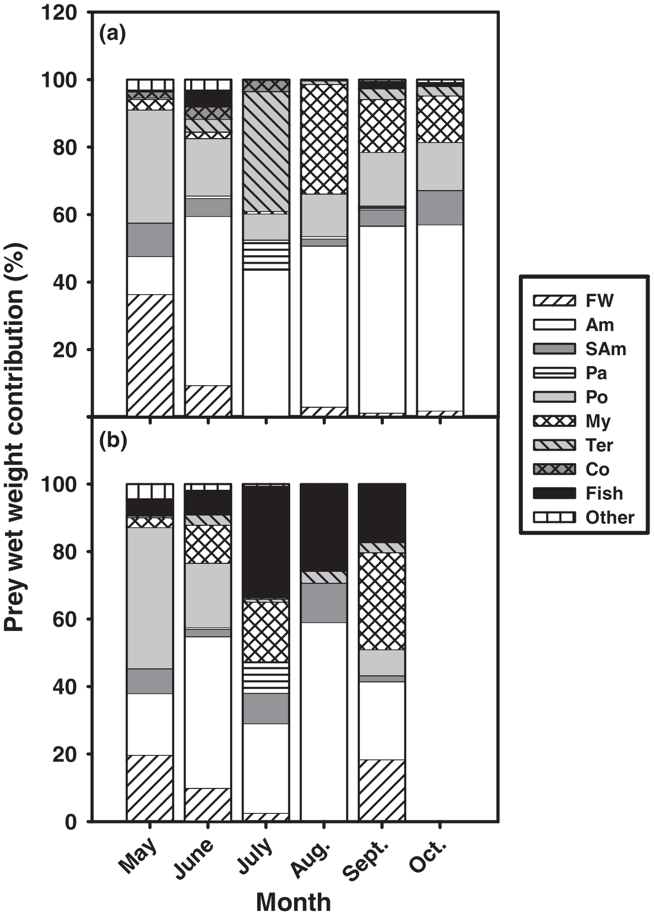
		First-year migrants		Second-year migrants	
Year	Month	*N*	Mean size (mm)	*N*	Mean size (mm)
1998	May	6	148 (14.9)	23	220 (44.5)
1999		12	114 (29.2)	76	240 (44.0)
2000		14	117 (24.2)	31	337 (86.7)
2001		86	118 (25.5)	71	248 (61.9)
2002		6	160 (16.1)	15	229 (32.9)
1998	June	23	177 (25.8)	10	224 (35.7)
1999		33	149 (34.1)	16	231 (40.3)
2000		49	122 (35.5)	47	247 (43.1)
2001		62	118 (28.2)	19	235 (57.6)
2002		19	121 (29.7)	—	—
1998	July	—	—	—	—
1999		9	147 (21.1)	—	234 (18.9)
2000		12	155 (33.0)	15	264 (35.4)
2001		17	122 (20.8)	4	256 (71.9)
2002		22	135 (28.6)	—	—
1998	August	15	212 (13.8)	—	—
1999		25	196 (25.9)	—	266 (24.4)
2000		14	177 (63.6)	4	274 (22.0)
2001		—	—	—	—
2002		—	—	—	—
1998	September	80	231 (32.6)	4	303 (10.6)
1999		78	221 (28.7)	11	275 (30.6)
2000		47	228 (32.1)	18	312 (26.6)
2001		11	201 (21.2)	3	304 (18.0)
2002		22	204 (33.8)	—	—
1998	October	56	228 (22.3)	—	—
1999		39	226 (22.5)	—	—
2000		14	211 (24.2)	—	—
2001		11	191 (25.7)	—	—
2002		26	226 (29.6)	—	—

upper SR, as prey fish %*W* ranged from 60% to 99% throughout the year. Freshwater aquatic invertebrate larvae were important in November, contributing 38% of the overall wet weight of contents. As shown previously, prey fish appeared mostly in trout larger than 25 cm in over 95% of stomachs (Fig. 5); the relative frequency of prey fish found in stomachs of second-year migrants increased significantly with size of second-year migrants ($F_{[1,16]} = 91.2$, $p < 0.001$, $r^2 = 0.85$; Fig. 5).

Ste. Marguerite River

Stomachs of trout from the SMR were obtained mostly in September and October, with the exception of one sampling year when trout were also sampled in February (Table 2). A total of 379 stomachs were obtained from first-year migrants in September and October, whereas 426 stomachs of second-year migrants were analysed, including those in February. For the months of September and October, 44.7% to 56.7% of first-year migrant stomachs were empty. Similarly, the %ES of second-year migrants ranged from 48.6% to 55.0% for September and October, with 90% of stomachs being empty in February. First-year migrants captured in the SMR containing food in their stomachs ($n = 156$) ranged in size from 241 to 262 mm (Table 7). For the second-year migrants captured in the river, 196 had food in their stomachs and ranged in size from 304 to 351 mm.

Fig. 4. Prey wet weight contribution to overall diet of (*a*) first-year and (*b*) second-year migrant brook trout (*Salvelinus fontinalis*) captured in estuarine Ste. Marguerite Bay (SMB) in 1998 to 2002 from May to October. Abbreviations: FW, freshwater aquatic invertebrate larvae; Am, amphipod; SAm, striped amphipod; Pa, panaeid shrimp; Po, polychaete; My, mysid shrimp; Ter, all terrestrial insects excluding coleopteran; Co, coleopteran; “Fish” includes sticklebacks, sand lance, smelt, and killifish; “Other” includes plant matter, winged insects (newly emerged), and all other miscellaneous items.



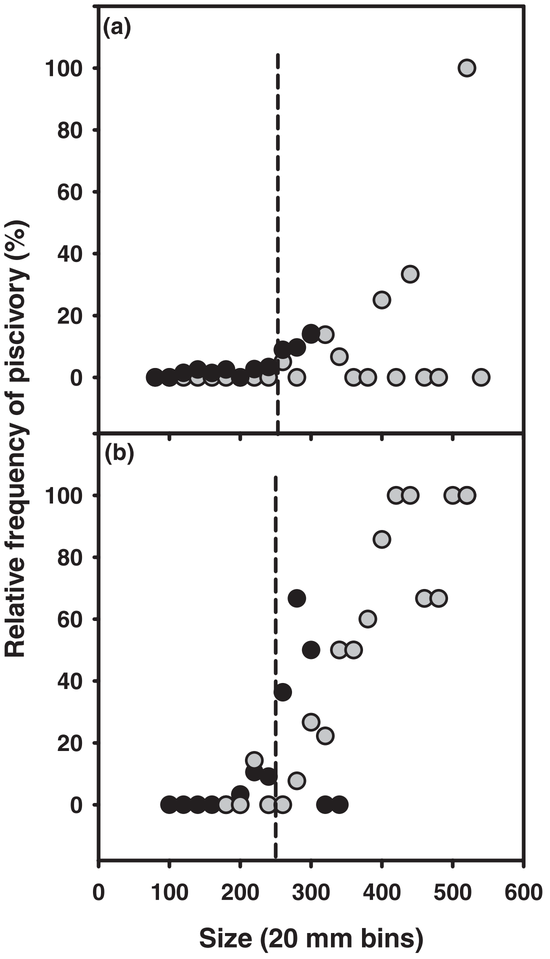
By wet weight, terrestrial insects made up the largest portion of the diet of first-year migrants captured in September, whereas in October, the diet consisted mostly of freshwater aquatic invertebrate larvae and salmonid eggs (Fig. 7). This is consistent with the two most dominant prey items occurring in the diet during these two months, with the exception of salmonid eggs (Table 8). Similarly, both freshwater aquatic larvae and terrestrial insects were frequently found in stomachs of second-year migrants in September, although the %*W* was highest for terrestrial insects, small mammal, and prey fish remains. In October, both freshwater aquatic invertebrate larvae and salmonid eggs made up a large proportion of the diet, consistent with the diet of first-year migrants.

Table 4. Number (*N*) of non-empty stomachs and percent occurrence (*%O*) of the two most dominant prey types (prey 1 and prey 2, respectively) found in stomachs (±1 standard error) from May to October (number of pooled years) of first- and second-year brook trout (*Salvelinus fontinalis*) migrants captured in Ste. Marguerite Bay (SMB) in years 1998 to 2002.

	Month	*N*	Prey 1	Prey 1 *%O*	Prey 2	Prey 2 *%O*
First-year	May (5)	124	FW	63.6 (12.7)	Po	31.7 (13.4)
	June (5)	186	Am	44.7 (6.9)	FW	26.4 (8.8)
	July (4)	60	Am	59.8 (15.0)	Ter	49.2 (17.1)
	August (3)	54	Am	66.4 (7.8)	My	48.8 (4.7)
	September (5)	237	Am	71.8 (7.5)	My	28.7 (9.3)
	October (5)	146	Am	68.3 (7.1)	My	28.7 (9.4)
Second-year	May (5)	216	FW	55.7 (14.4)	Po	45.1 (11.3)
	June (4)	91	Am	60.0 (8.6)	FW	24.4 (8.7)
	July (3)	21	Am	56.4 (6.4)	Pa	16.7 (16.7)
	August (2)	11	Am	64.3 (35.7)	SAm	21.4 (21.4)
	September (4)	36	Am	36.7 (15.7)	My	31.5 (5.2)

Note: FW, freshwater aquatic invertebrate larvae; Ter, terrestrial insects excluding coleopteran; Am, amphipod; SAm, striped amphipod; Po, polychaete; My, mysid; Pa, panaeid shrimp.

Fig. 5. Relative frequency of piscivory according to size in brook trout (*Salvelinus fontinalis*) migrants captured in (*a*) Ste. Marguerite Bay and (*b*) the Saguenay River. Solid circles and shaded circles refer to first- and second-year migrants, respectively. The broken line separates brook trout above and below the threshold of 25 cm.



Stable isotope analysis (SIA)

A significant positive relationship was found between stable carbon signatures (δ^{13}C) and fork length (FL) of first-year migrants (sea trout) captured in the SMB ($\delta^{13}C = 0.064FL - 29.4$; $F_{[1,74]} = 135.9$, $p < 0.0001$, $r^2 = 0.65$; Fig. 8). Similarly, a relationship was observed between δ^{13}C and FL for resident brook trout ($\delta^{13}C = 0.0062FL - 25.4$; $F_{[1,38]} = 6.1$, $p = 0.02$, $r^2 = 0.14$). The regressions between δ^{13}C and FL differed significantly between sea trout and resident brook trout both in slope (ANCOVA: $F_{[1,110]} = 26.5$, $p < 0.005$) and elevation (ANCOVA: $F_{[1,110]} = 6.6$, $p = 0.012$).

Significant relationships were also found between stable nitrogen signatures (δ^{15}N) and FL for sea trout ($\delta^{15}N = 5.2 + 0.036FL - 0.0001FL^2$; $F_{[2,74]} = 18.9$, $p < 0.001$, $r^2 = 0.34$) and for resident brook trout ($\delta^{15}N = 6.0 + 0.0051FL$; $F_{[1,35]} = 4.8$, $p = 0.04$, $r^2 = 0.10$). A significant difference in intercept exists between SMB trout up to 20 cm and resident brook trout (ANCOVA: $F_{[1,108]} = 176.5$, $p < 0.005$).

Marine invertebrate prey items captured in the SMB had signatures ranging from –17.8‰ to –15.6‰ for carbon and from 5.1‰ to 8.5‰ for nitrogen (Fig. 9). Signatures of prey fish, including sticklebacks, banded killifish, and smelt, were enriched in nitrogen compared with the marine invertebrate prey items, ranging from 10.5‰ to 14.0‰. Carbon was slightly depleted in comparison with the invertebrate prey. Freshwater insect larvae had typical signatures observed in freshwater systems. Amphipods obtained from Anse-à-Pierre, a more saline site located downstream of the SMB, had enriched carbon signatures but depleted nitrogen signatures compared with those of the SMB.

Upon sea entry, first-year migrants captured in the SMB in May had mean δ^{13}C and δ^{15}N signatures of –25.1‰ and 7.7‰, respectively. By October, trout mean δ^{13}C and δ^{15}N signatures rose to –14.5‰ and 9.1‰, respectively, and as expected, nitrogen signatures are 3.3‰ above marine invertebrate prey items, including amphipods and mysids. Sea-age-1 fish had mean δ^{13}C and δ^{15}N signatures of –14.7‰ and 9.8‰, respectively, whereas second-year migrants (both adult SMR system spawners and non-spawners) had signa-

Table 5. Number of non-empty stomachs (*N*) and mean size (±1 standard deviation) of first- and second-year brook trout (*Salvelinus fontinalis*) migrants captured from spring to winter in various sites located throughout the Saguenay Fjord and upper Saguenay River in pooled years 1998 to 2002.

	First-year migrants			Second-year migrants		
Month	Site	*N*	Mean size (mm)	Site	*N*	Mean size (mm)
March	—	—	—	CHIC	2	na
April	—	—	—	CHIC	1	283
May	—	—	—	AR	9	346 (107.8)
	—	—	—	AP	4	274 (93.3)
	—	—	—	VDLB	2	388 (46.7)
	—	—	—	CHIC	8	382 (68.9)
June	AR	11	173 (17.3)	AR	17	303 (98.8)
	AP	2	155 (1.4)	AS	10	254 (43.5)
	—	—	—	AP	7	271 (30.3)
	—	—	—	PS	4	na
	—	—	—	ASE	9	432 (64.9)
	—	—	—	CHIC	3	408 (106.5)
				SRN	2	454 (18.5)
July	ASE	3	180 (16.7)	ASE	8	334 (65.1)
	AI	11	142 (23.9)	AR	7	283 (24.5)
	AR	24	177 (43.9)	AS	8	269 (52.4)
	AS	23	159 (30.1)	AP	6	282 (25.2)
	—	—	—	VDLB	1	481
August	AP	18	164 (29.6)	AS	7	274 (48.7)
	AS	8	198 (29.6)	AP	3	268 (10.0)
	AI	2	214 (20.5)	ASE	2	308 (21.2)
	AL	6	188 (64.9)	—	—	—
	AG	13	135 (9.2)	—	—	—
September	AS	4	201 (29.5)	APOR	2	287 (24.8)
	AI	2	234 (31.8)	AS	2	285 (20.5)
	APOR	11	229 (12.2)	—	—	—
October	CHIC	4	219 (32.1)	—	—	—
November	CHIC	2	191 (27.6)	CHIC	2	356 (5.7)
December	CHIC	3	na	VDLB	1	345
	—	—	—	CHIC	5	365 (27.6)
January	CHIC	9	247 (25.9)	CHIC	2	389 (102.5)
February	CHIC	4	273 (23.2)	CHIC	4	390 (38.4)

Note: na, not applicable. Site abbreviations: AR, Anse-de-Roche; AP, Anse-à-Pierre; ASE, Anse-Ste- Étienne; AI, Anse-aux-Petites-Îles; AS, Anse-de-Sable; AL, Anse-à-l'Île; AG, Anse à Gagnon; APOR, Anse-du-Portage; CHIC, Chicoutimi (now City of Saguenay); VDLB, Ville-de-la-Baie (now City of Saguenay); PS, Petit Saguenay; SRN, Ste-Rose-du-Nord.

tures of about –17.8‰ for carbon and about 12.3‰ for nitrogen.

Discussion

Anadromous brook trout migrating to the SR from the SMR more than double their size over the course of a summer spent at sea (Lenormand et al. 2004). It is expected that for trout to experience such rapid growth rates, the sea must provide better feeding opportunities than freshwater. Such opportunities may come in the form of overall higher productivity and (or) a higher occurrence of large prey (Keeley and Grant 2001), which also includes increased accessibility to such prey. Our results confirmed this prediction, as the SMB, the trout's initial site of sea entry, exhibited better food opportunities (in terms of prey size) than the SMR. Mean invertebrate biomass estimates did not differ between the SR and the SMB in either May or August. However, invertebrates in the SMB were 2.4 times and 2.2 times larger than those found in the SR in both May and August, respectively. Moreover, it was seen that within specific taxonomic groups, a lower proportion of individuals in freshwater sites comprised the larger size classes compared with those occurring in marine sites. Potentially having immediate access to more energetically profitable prey (increasingly larger prey) permits an efficient growth return, because fewer items need to be consumed (and thus captured) to acquire the same amount of energy (Pazzia et al. 2002; Sherwood et al. 2002). Moreover, growth benefits can be materialized more rapidly because the migration, and thus shift to larger prey, follows soon after a period of overwintering and starvation.

Interestingly, a wider range of prey sizes was also observed in the bay versus in the river, indicating that newly arrived fish are presented with a broader range of feeding

Fig. 6. Prey wet weight contribution to overall diet of (*a*) first- and (*b*) second-year migrant brook trout (*Salvelinus fontinalis*) captured in estuarine Saguenay River (fjord and upper Saguenay) from 1998 to 2002 across months. Abbreviations: FW, freshwater aquatic invertebrate larvae; Am, amphipod; SAm, striped amphipod; Pa, panaeid shrimp; Po, polychaete; My, mysid shrimp; Ter, all terrestrial insects excluding coleopteran; Co, coleopteran; "Fish" includes sand lance and smelt; "Other" includes plant matter, winged insects (newly emerged), and all other miscellaneous items.

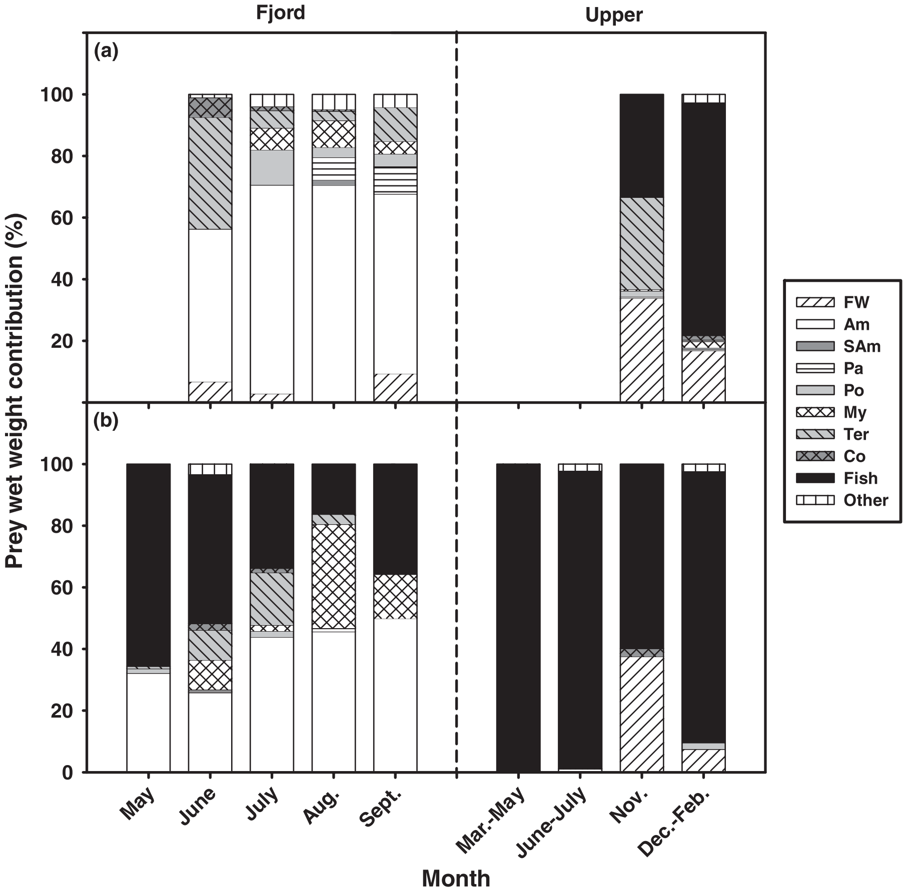


Table 6. Number (*N*) of non-empty stomachs and percent occurrence (%*O*) of the two most dominant prey types (prey 1 and prey 2, respectively) found in stomachs (±1 standard error) from spring to winter (number of pooled sites) of first- and second-year brook trout (*Salvelinus fontinalis*) migrants captured in sites located in the Saguenay Fjord and upper Saguenay River in years 1998 to 2002.

	Site	Month	*N*	Prey 1	Prey 1 %*O*	Prey 2	Prey 2 %*O*
First-year	Saguenay Fjord	June (2)	13	Ter	62.5 (26.5)	Am	54.2 (2.9)
	Saguenay Fjord	July (4)	61	Am	75.0 (6.3)	Ter	16.4 (7.2)
	Saguenay Fjord	August (5)	47	Am	61.9 (12.0)	My	37.8 (8.4)
	Saguenay Fjord	September (3)	17	Am	57.9 (4.1)	Ter	23.3 (14.5)
	Upper Saguenay	October–November (2)*	6	Ter; FW	75.0 (25.0)	—	—
	Upper Saguenay	December–January–February (3)*	16	Fish	65.7 (16.7)	FW	31.5 (11.3)
Second-year	Saguenay Fjord	May (2)	13	Am	52.5 (22.5)	Fish	37.5 (12.5)
	Saguenay Fjord	June (6)	49	Fish	40.1 (18.4)	Ter	30.6 (13.0)
	Saguenay Fjord	July (4)	29	Ter	43.8 (7.7)	Am	41.7 (15.3)
	Saguenay Fjord	August (3)	12	Am	57.1 (29.7)	My	38.1 (31.2)
	Saguenay Fjord	September (2)	4	Am	50 (50)	My; Fish	25 (25)
	Upper Saguenay	March–April– May (4)†	13	Fish	96.9 (3.1)	FW	21.9 (12.9)
	Upper Saguenay	June–July (2)†	4	Fish	100 (0)	FW	33.3 (33.3)
	Upper Saguenay	November (1)†	2	Fish; FW; Co	50	—	—
	Upper Saguenay	December–January–February (4)†	10	Fish	78.8 (14.2)	FW	21.3 (14.2)

Note: FW, freshwater aquatic invertebrate larvae; Co, coleopteran; Ter, terrestrial insects excluding coleopteran; Am, amphipod; SAm, striped amphipod; My, mysid; Fish, includes sand lance and smelt.

*Only includes Chicoutimi (CHIC) site.

†Includes both Chicoutimi (CHIC) and Ville de la Baie (VDLB) sites.

Table 7. Number of non-empty stomachs (*N*) and mean size (±1 standard deviation) of first- and second-year brook trout (*Salvelinus fontinalis*) migrants captured in the Ste. Marguerite River following seaward migration from September to October in years 1998 to 2000.

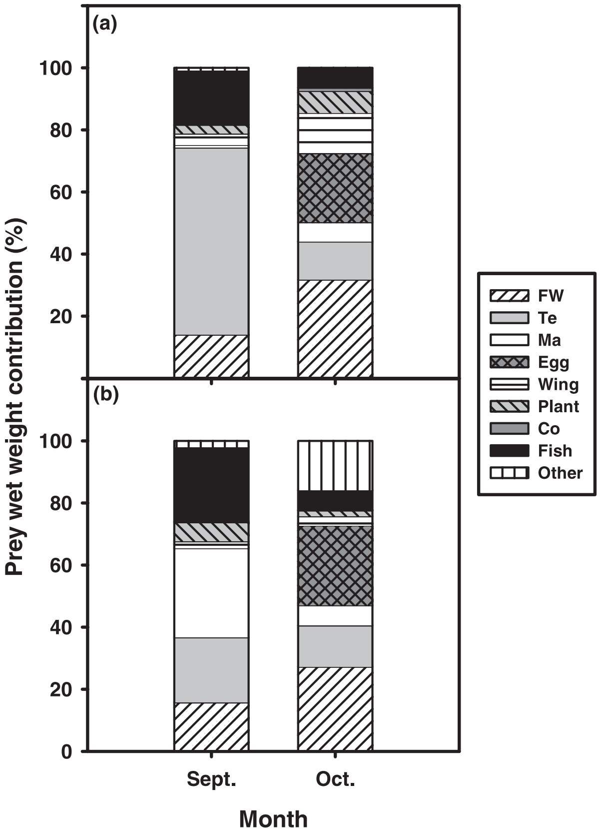
		First-year migrants		Second-year migrants	
Year	Month	*N*	Mean size (mm)	*N*	Mean size (mm)
1998	September	62	256 (26.9)		39
1999		16	249 (27.5)	34	326 (28.6)
2000		6	256 (19.2)	13	304 (37.9)
1998	October	44	256 (19.5)	40	330 (44.0)
1999		23	262 (26.0)	53	341 (44.1)
2000		5	241 (18.8)	17	353 (60.2)

opportunities. The presence of a larger available prey spectrum is also important as it can serve the needs of a wider predator size range and, in turn, limit intraspecific competition for similarly sized prey, because fish generally consume larger prey with increasing size when available (Werner and Gilliam 1984; Keeley and Grant 1997, 2001).

Anadromous brook trout migrating to sea for the first time (first-year migrants) capitalized almost immediately on the better feeding opportunities available in the SMB. Less than 15% of trout sampled in the bay contained an empty stomach, suggesting high feeding activity. Their initial food at sea reflected the transition to a saline habitat from a freshwater habitat. Upon sea entry in May, first-year migrants initially consumed freshwater-derived prey, a conclusion based on the frequency of occurrence and percent wet weight contribution of aquatic insect larvae. This is consistent with earlier reports of high occurrences of aquatic invertebrate larvae also being found in stomachs of brook trout recently entering the sea (Gaudreault et al. 1982; O'Connell 1982). The initial high occurrence of freshwater-derived prey in addition to polychaetes, located mostly in the sand and clay flats surrounding the main river channel outflow (G.R. Morinville, personal observation), agrees with the need of first-time migrants to remain under the influence of the natal river to minimize the costs associated with osmoregulation (McCormick et al. 1985; Lenormand et al. 2004).

By June, first-year migrants inhabiting the SMB rapidly shifted to a diet composed of larger prey, obtaining over 60% of their energy from amphipods and polychaetes within a few weeks of sea entry, consistent with previous reports of feeding behaviours (White 1940, 1942). These amphipods were generally of medium sizes, ranging in length from 5 to 13 mm (G.R. Morinville and J.B. Rasmussen, unpublished data). This feeding pattern was observed in trout exploiting the bay for the remaining summer months and early fall, where at least 50% of the energy was derived from amphipods in addition to prey items such as mysids and polychaetes. The frequent ingestion of mysids later in the summer suggests a surface-oriented feeding position close to shore (Montgomery et al. 1990). Amphipods in addition to sand lance were also the dominant prey items in trout sampled between late August and early October in the Matamek River estuary (Whoriskey et al. 1981). These observations were also consistent with earlier studies involving the anadromous form of brown trout (*Salmo trutta*) and Arctic char (*Salvelinus alpinus*) (Moore and Moore 1974; Pemberton 1976; Knutsen et al. 2001). Other than a few occurrences of sticklebacks and sand lance in the spring and fall, fish were infrequently encountered in stomachs of first-year migrants captured in the SMB. Similarly, second-year migrants, having spent at least one previous summer at sea, returned to the deeper waters of the Saguenay fjord, passing through the SMB during the month of May. As with first-year migrants, they initially fed on polychaetes and aquatic invertebrate larvae during their descent into the bay, although by June, their diet was composed mostly of marine crustaceans (amphipods).

Fig. 7. Prey wet weight contribution to overall diet of (*a*) first- and (*b*) second-year migrant brook trout (*Salvelinus fontinalis*) captured in Ste. Marguerite River from 1998 to 2000 in September and October. Abbreviations: FW, freshwater aquatic invertebrate larvae; Ter, all terrestrial insects excluding coleopteran; Ma, small mammals; "Egg" includes eggs of either brook trout or Atlantic salmon (*Salmo salar*); "Wing" includes newly emerged flies and adult flies; "Plant" includes all plant matter; Co, coleopteran; "Fish" includes sand lance and smelt; "Other" includes plant matter, winged insects (newly emerged), and all other miscellaneous items.



First-year migrants that ventured into the Saguenay fjord also had a diet composed mainly of amphipods, contributing over 50% to their diet, in addition to terrestrial insects and mysids. These trout acquired an orange–pink flesh over the course of the summer, confirming a diet composed of carotenoid-rich marine crustaceans (Peterson et al. 1966). No piscivorous first-year migrants feeding in the fjord (not

Table 8. Total number (*N*) and percent occurrence (*%O*) of the two most dominant prey types (prey 1 and prey 2, respectively) found in stomachs (±1 standard error) from September to October (number of pooled years) of first- and second-year brook trout (*Salvelinus fontinalis*) migrants captured in the Ste. Marguerite River (SMR) in years 1998 to 2002.

	Month	*N*	Prey 1	Prey 1 *%O*	Prey 2	Prey 2 *%O*
First-year	September (3)	84	Ter	60.3 (24.0)	FW	42.0 (13.4)
	October (3)	72	FW	68.7 (8.4)	Plant	16.9 (10.1)
Second-year	September (3)	86	FW	59.9 (6.7)	Ter	23.1 (8.3)
	October (3)	110	FW	52.4 (11.7)	Ter	23.6 (8.9)

Note: FW, freshwater aquatic invertebrate larvae; Ter, all terrestrial insects excluding coleopteran; Plant, includes all plant matter.

Fig. 8. Stable carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) signatures as a function of fish length (FL) for sea trout (anadromous brook trout (*Salvelinus fontinalis*); solid circles) captured in the Ste. Marguerite Bay ($\delta^{13}C = 0.064FL - 29.4$, $p < 0.0001$, $r^2 = 0.65$; $\delta^{15}N = 5.2 + 0.036FL - 0.0001FL^2$, $p < 0.001$, $r^2 = 0.34$) and for resident brook trout (open circles) captured in Morin Stream, a tributary of the Ste. Marguerite River ($\delta^{13}C = 0.0062FL - 25.4$, $p = 0.02$, $r^2 = 0.14$; $\delta^{15}N = 6.0 + 0.0051FL$, $p = 0.04$, $r^2 = 0.10$). Sea trout were captured from May to September. Resident trout were captured in June and July.

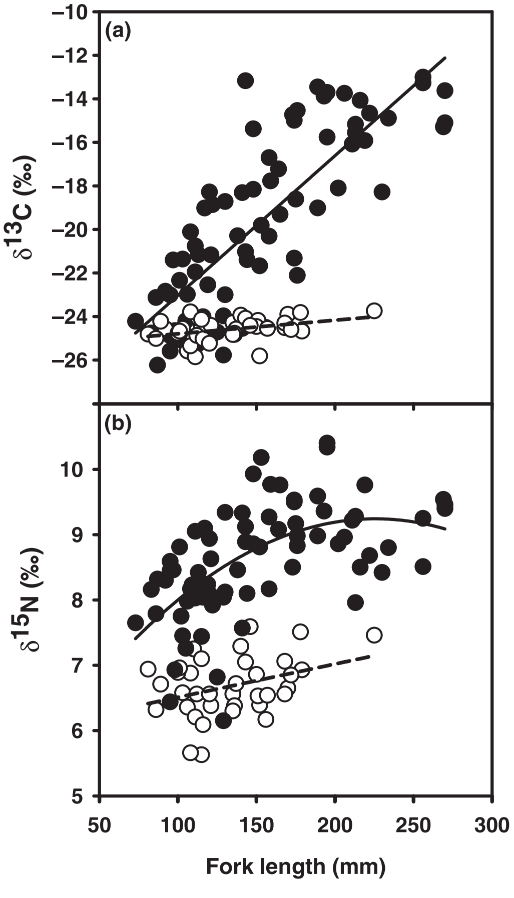
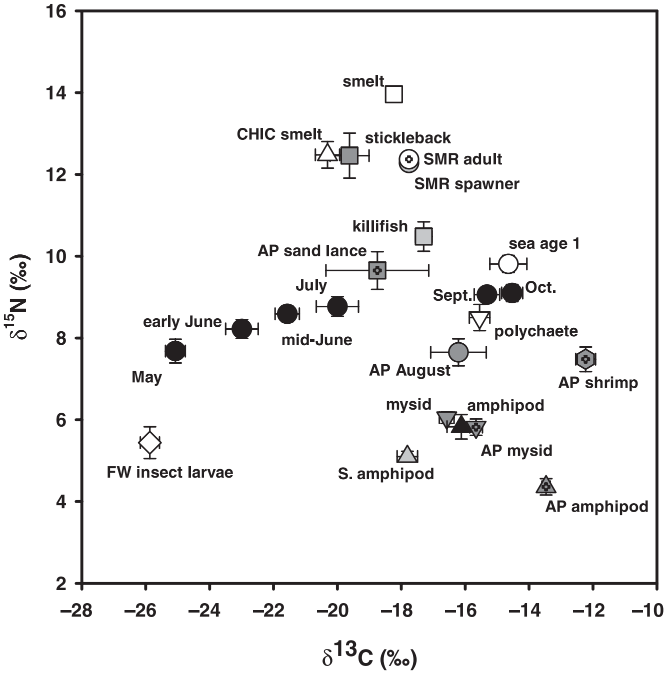


Fig. 9. $\delta^{15}N$ and $\delta^{13}C$ of anadromous brook trout (sea trout, *Salvelinus fontinalis*) from the Ste. Marguerite River system, Quebec. May, early and late June, July, September (Sept.), and October (Oct.) indicate the mean signature of first-year sea trout captured in the Ste. Marguerite Bay (SMB) during those months. "AP" August and "AP" prey items refer to isotope signatures of first-year migrants and prey items captured in Anse-à-Pierre (Saguenay River), respectively, which is located downstream of the SMB. Sea-age-1 refers to sea trout captured in the SMB in early May that are beginning their second summer at sea; FW, freshwater; S., striped; SMR spawner and adult refers to an anadromous brook trout spawner and nonspawner captured in the Ste. Marguerite River; CHIC smelt, smelt found in the stomach of a trout captured in CHIC (upper Saguenay River site).



including the SMB or upper SR) were ever encountered in the 5 years of study. This contrasts with the diet of second-year migrants inhabiting the fjord and upstream regions of the SR. Similarly, fish made up only a minor component of the diet of first-year Arctic char, brown trout, and St. John River brook trout migrants, whereas second-year migrants fed more heavily on fish (Gaudreault et al. 1982; Rikardsen and Elliott 2000; Knutsen et al. 2001).

The rapid shift to marine prey items in first-year migrants was clearly observed with stable isotope signatures of trout muscle tissues. Between May and October, the $\delta^{13}C$ signature of first-year migrants increased by more than 10‰ from a freshwater signature of –25‰ to a more marine signature of –14.5‰. This change was detected with increasing trout size. As expected, such abrupt changes in $\delta^{13}C$ were not observed in resident brook trout with increasing size. The diet of trout remaining in freshwater streams, as revealed by stomach content analyses, indicated no important change of diet with ontogeny because trout continued to feed mostly on freshwater aquatic invertebrates and some terrestrial insects (G.R. Morinville, unpublished data).

δ^{15}N signatures of first-year migrants also changed with size, increasing from 7.7‰ to 9.1‰ by October. Slight increases were also observed in resident brook trout, possibly reflecting a shift to larger and slightly higher level prey items, such as predatory caddisfly. In the SMB, amphipods had δ^{13}C and δ^{15}N signatures averaging –16‰ and 5.8‰, respectively, whereas mysids had signatures averaging –16.6‰ and 6.1‰, respectively. Given the expected fractionation between prey and predator of about 0‰–1‰ for carbon and about 3‰–4‰ for nitrogen (DeNiro and Epstein 1978; Minagawa and Wada 1984; Peterson and Fry 1987) and the information obtained from stomach content analyses, amphipods and mysids appeared to be the main prey items from which first-year migrants obtained their energy.

Trout (first-year migrants) that migrated to the upstream sections of the SR to overwinter in freshwater had a diet consisting primarily of fish and freshwater aquatic invertebrate larvae in late autumn, followed by a diet made up almost entirely of fish (mostly smelt) in the winter months. Similarly, Knutsen et al. (2001) also reported higher occurrences of fish in the diet of anadromous brown trout during autumn. In this study, the shift to piscivory occurred when sea trout reached sizes of at least 20 cm, with a relative frequency of piscivory of 50% occurring at 25 cm. Prey fish also predominated in stomachs of sea trout larger than 30 cm in length captured in coastal waters of Newfoundland, Richmond Gulf (Quebec), and the St. John River (Quebec) (Dutil and Power 1980; O'Connell 1982). Pemberton (1976) also found that brown trout larger than 21 cm had higher occurrences of fish in their diet than those smaller than 21 cm, which consumed primarily crustaceans and insects.

Trout migrating to the upper Saguenay remained actively feeding (less than 20% empty stomachs), instead of returning to their natal river, obtaining high-energy returns throughout the winter months and allowing them to maintain their condition. In contrast, those returning to their natal river during fall decreased their feeding activity (50% empty stomachs), feeding mainly on small, low-energy prey, including terrestrial insects and aquatic invertebrate larvae, consistent with the diet of anadromous brown trout returning to freshwater (Harris 1971). Traces of fish (either trout or salmon) and small mammals, in addition to salmonid eggs, were noted in a fraction of stomachs, supporting the observation of their opportunistic feeding behaviour (Power 1980), although sea trout still tended to be of poor condition upon their return to sea following winter (Lenormand et al. 2004).

Interestingly, trout having spent the previous summer at sea and captured the following spring had a similar δ^{13}C signature as those captured at the end of October, indicating no change in feeding habits or habitats over winter. The slightly heavier δ^{15}N signature in comparison with the October trout may reflect a starvation effect leading to enrichment (Vander Zanden and Rasmussen 2001), inferred from the observation that trout descending the river in spring are of lower condition than those that overwintered in and continued to feed in the upper SR (Lenormand et al. 2004). The effect of starvation may also explain the 1‰ difference in δ^{15}N observed between first-year migrants and residents at small sizes because differences in diet during their coexistence in streams are unlikely.

Although δ^{15}N of first-year migrants increased with size during the course of the summer, the change was not linear. Instead, it followed a curvilinear pattern with increasing size, reaching a high of around 20 cm in length and decreasing slightly thereafter. This is expected to occur following a rapid shift in diet because tissue signatures approach new prey signatures asymptotically over time, because of the time lag resulting from the residual pool of tissues with the old signature. Moreover, the non-linear pattern may also be reflecting changes in feeding location. As mentioned earlier, trout during the summer exited the SMB and migrated to neighbouring sites across the Saguenay, including the downstream Anse-à-Pierre and Anse-de-Roche sites. First-year migrants initially captured in the SMR system have been frequently recaptured in these locations (Lenormand et al. 2004). As indicated by SIA, migrants continued to feed heavily on marine amphipods at these sites and throughout the Saguenay fjord. Marine amphipods collected in AP were found to be more enriched in δ^{13}C but lighter in δ^{15}N compared with those in the SMB. It is thus quite likely that trout, when feeding outside of the SMB and in the fjord, acquired the signature of amphipods found in sites such as Anse-à-Pierre before their return to the SMB in the fall, leading to the observed curvilinear pattern with increasing size. This is likely as trout (not necessarily originating from the SMR system) captured in August in Anse-à-Pierre had lower δ^{15}N signatures than those captured in the SMB in July.

It is important to mention that second-year migrants captured in the SMB from July to September were likely returning from earlier migrations to the greater SR. These trout were possibly future spawners (Lenormand et al. 2004) and may have started reducing their energy intake upon return to the bay, although some may have continued eating amphipods and fish. This has been previously reported in sea trout populations of the Moser River (Nova Scotia), in which over 50% had empty stomachs, and of those with contents, 27% were almost empty (Wilder 1952). Indeed, the percentage of empty stomachs of second-year migrants was highest in the bay during the months of August and September, reaching levels of almost 40%. Those that continued upstream into the SMR presumably further reduced their feeding activity, because over 50% of captured trout had empty stomachs in the fall. Over 80% of sea trout likely to spawn and captured on the spawning grounds also had empty stomachs (G.R. Morinville and J.B. Rasmussen, unpublished data). Similarly, White (1940) also reported no food in the stomachs of ascending trout. In winter, over 75% of second-year migrants captured in the SMB or SMR had empty stomachs, suggesting older migrants in winter virtually ceased feeding until the following spring. This reduced feeding behaviour may explain the low condition factor of trout descending the river in early spring (Lenormand et al. 2004).

Anadromous brook trout have previously been considered largely piscivorous (Power 1980), although these conclusions were based on earlier reports of feeding that failed to consider the size at which piscivory begins or whether fish eating occurred on a seasonal basis. For all sampled habitats, piscivorous trout generally exceeded 25 cm in length, consistent with other salmonid populations (Keeley and Grant 2001). This threshold of piscivory was consistent regardless of whether trout were in their first or more years at sea. Moreover, high occurrences of frequent piscivory generally occurred in specific locations of the Saguenay River, notably the upper SR (CHIC and VDLB sites), and during specific seasons, winter and spring, with smelt being the dominant fish species in trout stomachs (G.R. Morinville, personal observation). In winter, smelt may be more susceptible to predation by trout as the activity of smelt is lowered under ice cover (Vinni et al. 2005), whereas in the spring, smelt migrate upstream for spawning (Pigeon et al. 1998). Seasonal dependence on fish in the diet has also been reported in anadromous brown trout, where fish were by mass the dominating prey during winter feeding, likely reflecting prey availability during those months (Knutsen et al. 2004).

Stable isotope signatures of SMR adult migrant spawners and non-spawners indicated that the sea trout never fully became piscivorous on smelt. This was inferred from the dual isotope approach in which migrants had lighter $\delta^{13}C$ (difference of 2.5‰) but similar $\delta^{15}N$ signatures to those of the upper SR smelt. If smelt had contributed fully to the diet of sea trout, we would have expected trout to reach a $\delta^{15}N$ signature of about 3.4‰ above the smelt signature, given the fractionation between predator and prey (Minagawa and Wada 1984; Vander Zanden and Rasmussen 2001); however, this was not observed. Muscle tissue $\delta^{15}N$ signatures of sea trout from the SMR system seldom go beyond 14‰ (G.R. Morinville and J.B. Rasmussen, unpublished data). Such signatures were largely supported by SCA as second-year migrants continued to feed on amphipods and mysids during the summer across the SMB and fjord. Sea trout of the St. John River (Quebec) were also reported to feed heavily on amphipods throughout the year, even at large sizes, although fish contributed highly to the summer diet (Gaudreault et al. 1982). Alternatively, migrants could also be feeding heavily on sand lance, as $\delta^{15}N$ signatures of sand lance were approximately 2.8‰ lower than those of adult migrants.

Few competitors are present where brook trout enter the sea. Both sticklebacks and banded killifish can be found in the SMB, with sticklebacks being the most abundant permanent resident species of the bay (Mousseau and Dodson 1996). However, threespine sticklebacks in the bay are relatively small (5–8 cm FL; M. Bélanger and J.B. Rasmussen, unpublished data). Both SCA and SIA indicated that sticklebacks captured in the SMB between May and July consumed mostly marine amphipods and freshwater aquatic invertebrate larvae, depending on their proximity to freshwater (M. Bélanger and J.B. Rasmussen, unpublished data). First-year migrants were also found to eat such prey items, although migrants entering the SMB were, on average, larger than sticklebacks, ranging in size from 7 to17 cm (Lenormand et al. 2004). Given their larger size and the wider prey spectrum available in the bay, it is unlikely that trout strongly competed with sticklebacks for the same prey size categories. However, stronger competitive interactions could develop over time if trout were to migrate at increasingly smaller sizes, a situation that could arise following increasingly poor growth conditions in freshwater before migration.

In conclusion, marine crustaceans, mostly amphipods, were the most important prey item in the diet of first-year migrants, allowing them to experience rapid growth rates during their first summer spent at sea. During their ontogeny, migrants, whether they were in their first year at sea or greater, shifted their dependence to prey fish at the threshold size of 25 cm. First-year migrants generally reached these sizes after their first summer of growth, allowing them to benefit from energy-rich fish (mostly smelt) in the first winter, provided they migrated to the upper SR for winter. The highest levels of piscivory occurred in the upper SR sites, signifying this region as an essential feeding ground for sea trout, allowing for continual growth. Of concern, the agglomeration of sea trout in these feeding grounds during winter and early spring makes sea trout especially vulnerable to overfishing and habitat destruction. As a consequence, strict regulations need to be implemented, including both the protection of feeding grounds and limits to fishing during these months. Additional regulations protecting the prey base of sea trout also need to be implemented to preserve the anadromous form.

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