

To fast or feed: an alternative life history for anadromous brook trout *Salvelinus fontinalis* overwintering within a harbour

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The seasonal feeding pattern of sea-run brook trout *Salvelinus fontinalis* was studied from November to May 2010–2012 in Antigonish Harbour, Nova Scotia, Canada (45° 38' N; 61° 55' W). Sixty-three *S. fontinalis* (mean ± s.d. fork length = 330 ± 70 mm and mass = 536 ± 351 g) captured had fed predominantly on fishes (Fundulidae and Gasterosteidae). Percentage of empty stomachs was highest during autumn (18%) and winter (22%) and lowest in spring (7%). Stomach fullness increased from autumn to a maximum during winter, relating to near-zero body temperatures which may have effectively stopped gastric evacuation. Although feeding occurred during winter (December to March), consumption rates were calculated as negative values, and subsequently returned to positive values in spring (April to May). The over-winter life-history strategy of this sea-run *S. fontinalis* population appears to be a feeding marine migration in which fish continually increase body condition, representing an alternative to the more common overwintering strategy of starvation in fresh water until spring.

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Key words: body condition; body temperature; consumption rates; marine migration; seasonal diet; stomach fullness.

INTRODUCTION

The marine migration of salmonids is largely driven by more favourable feeding conditions leading to rapid growth, enhanced fecundity and increased survival (Nikolsky, 1963; Harden Jones, 1968; Northcote, 1978, 1984). Most marine migrations commence in spring with a return to fresh water for autumn spawning, and overwintering for iteroparous species, with migrants often decreasing or ceasing feeding activity within fresh water (Klemetsen *et al.*, 2003; Quinn, 2005; Thorstad *et al.*, 2011). There are, however, documented accounts of Atlantic salmon *Salmo salar* L. 1758, brown trout *Salmo trutta* L. 1758 and Arctic char *Salvelinus alpinus* (L. 1758) populations residing in brackish to full-strength sea water during winter (Jonsson & Jonsson, 2002;

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Rikardsen *et al.*, 2006; Jensen & Rikardsen, 2008, 2012; Lacroix, 2013). It has also been observed that some anadromous brook trout *Salvelinus fontinalis* (Mitchill 1814) return to estuaries in autumn and remain there over winter (Bigelow & Welsh, 1925; Smith & Saunders, 1958; Gaudreault *et al.*, 1982; Curry *et al.*, 2002; Morinville & Rasmussen, 2006). This appears to be the case for an anadromous population of *S. fontinalis* overwintering in Antigonish Harbour, Nova Scotia, Canada.

Few studies have documented the marine diet of anadromous *S. fontinalis*, and most of them only provide a description of prey items found in stomachs, such as crustaceans (especially *Crangon* sp., *Gammarus* sp. and *Mysis* sp.), insects, mammals (deer mouse *Peromyscus* sp.) and polychaetes *Nereis* sp. Fishes consumed included capelin *Mallotus* sp., hake *Urophycis* sp., killifishes (Fundulidae), *S. fontinalis*, sand lance *Ammodytes* sp., sculpins (Scorpaeniformes), smelt *Osmerus* sp., sticklebacks (Gasterosteidae), rock gunnel *Pholis* sp. and whitefishes *Coregonus* spp. (White, 1940, 1942; Dutil & Power, 1980; Gaudreault *et al.*, 1982; O'Connell, 1982; Morinville & Rasmussen, 2006). Morinville & Rasmussen (2006) found crustaceans and fishes to be the dominant prey items for first and second year migrants, respectively, with *S. fontinalis* >250 mm fork length, L_F , showing piscivory.

Only two studies in the north-west Gulf of St Lawrence (48° N) documented estuarine winter feeding (Gaudreault *et al.*, 1982; Morinville & Rasmussen, 2006). There are apparently no diet studies of *S. fontinalis* populations overwintering in estuaries of the southern Gulf (45° N). To address the lack of detailed knowledge on marine migration and life-history strategies of northern anadromous salmonids, including information during winter (Huusko *et al.*, 2007), this study aimed to (1) describe the diet of *S. fontinalis* from autumn to spring and (2) determine if *S. fontinalis* are feeding under sea ice during winter. To do this, seasonal changes in diet and feeding intensity (% empty stomachs, stomach fullness, consumption rates and body condition) of *S. fontinalis* captured within Antigonish Harbour from November to May were examined. It was hypothesized that *S. fontinalis* diet would vary with the seasons, with piscivory occurring in migrants >250 mm L_F , with winter feeding focused on *Osmerus* sp. that are abundant from December to January. Feeding intensity during winter was expected to decrease with cold water temperatures, with percentage of empty stomachs being the highest, and stomach fullness and consumption rates being the lowest. Body condition was expected to be lowest in autumn and increasing until the end of the migration in late-spring.

MATERIALS AND METHODS

STUDY SITE

Antigonish Harbour, Nova Scotia, Canada (45° 38' N; 61° 55' W), is a semi-enclosed, Y-shaped, estuarine system with three rivers draining into the inner harbour, the South River in its southern end and the West and Wrights Rivers in its western extent (Fig. 1). The inner harbour is characterized by a shallow (water depth, Z , <2 m), silted, cordgrass *Spartina* sp. salt-marsh delta containing numerous inlets, coves and tidally influenced ponds. The mid-harbour has shallow inlets and multiple islands with a deep basin (Z_{\max} = 11 m) and channels (Z < 3 m) fringed with blue mussels *Mytilus* sp and American oysters *Crassostrea* sp. The outer harbour is dominated by a barrier beach with two channels (Z < 5 m) connecting to St George Bay, Gulf of St Lawrence. The outer harbour contains multiple islands, shallow shoals blanketed by eel grass *Zostera* sp. (Thériault *et al.*, 2006) and a large salt-marsh pond. The harbour is known to

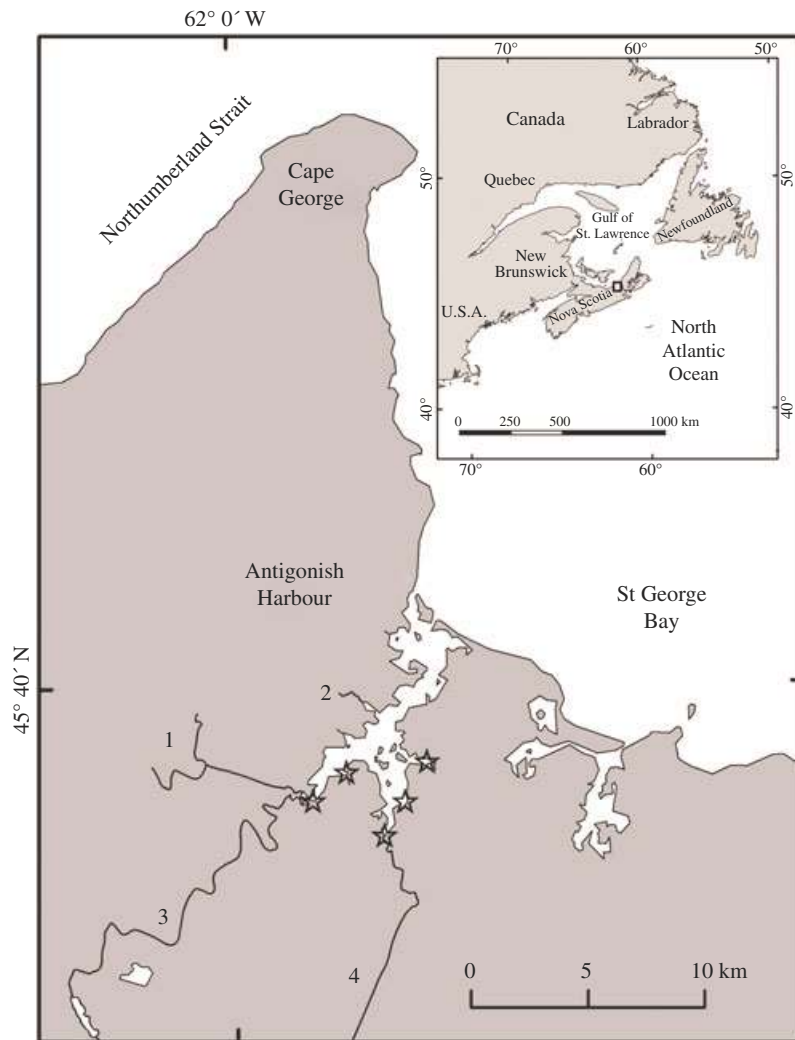


Fig. 1. Location of Antigonish Harbour, Nova Scotia, Canada, showing capture sites (☆) of sea-run *Salvelinus fontinalis* during late-autumn to mid-spring 2010–2012, and the (1) Wrights, (2) North, (3) West and (4) South Rivers.

contain a population of sea-run *S. fontinalis* which support a popular recreational spring fishery (MacMillan & Madden, 2007).

FISH SAMPLING

A total of 63 *S. fontinalis* were captured during day and night with a 5.1 cm stretched mesh gillnet, live-trap fyke net, rod and obtained opportunistically from fishers, from 19 November to 5 May 2010–2012. No captures occurred in February. Autumn samples were captured near the head of the tide in the South and West Rivers using fyke and gillnets ($n = 11$). Winter samples were captured by ice rod at the east harbour in January ($n = 6$) and by gillnet near the head of

the tide in the West River in March ($n = 3$). Spring samples were caught throughout the inner harbour ($n = 43$), with the majority captured in West and South River estuaries (Fig. 1).

The L_F to the nearest mm and mass (M), including stomach contents, to the nearest 10 g were recorded. Excised stomachs were individually wrapped, labelled and stored on ice until freezing at -20°C . In the laboratory, stomachs were thawed, contents removed, separated and identified to family (Carlander, 1950; Borror & DeLong, 1954; Needham & Needham, 1962; Bromley & Bleakney, 1984; Marshall, 2006) or alternative grouping (*i.e.* fish remains). Due to advanced digestion, some contents were numerically estimated from identifiable body parts (Power *et al.*, 2002). Excess moisture was blotted dry prior to counting and weighing (nearest 0.001 g).

STOMACH CONTENT ANALYSIS

Samples were pooled according to season: autumn (22 September to 20 December), winter (21 December to 19 March) and spring (20 March to 20 June), combining all collection years due to low sample sizes (Morinville & Rasmussen, 2006). For all samples and seasonal categories, indices of occurrence ($\%O$), number ($\%N$) and mass ($\%M$) were used to determine frequency and relative importance of each prey type consumed (Hyslop, 1980). The diet of an individual was quantified using the index of relative importance (I_{RI}) calculated for each taxon, excluding vegetal matter. The I_{RI} is defined as: $I_{RI} = (\%N + \%M) \%O$; where $\%N$ is the per cent number of certain prey item, $\%M$ is the per cent mass and $\%O$ is the frequency of occurrence (McLean *et al.*, 2013). The diets of *S. fontinalis* >250 mm L_F were examined for piscivory. Further seasonal diet differences were compared using total number of taxa, mean number of taxa and the Shannon–Weiner and Schoener overlap indices. The Shannon–Weiner diversity index (H') was calculated as: $(H') = -\sum_i^n p_i \ln p_i$, where p_i is the mean $\%M \times 0.01$ of taxon i . Diet overlap between seasons was compared with Schoener's overlap index (I_S), so that: $I_S = 1 - 0.5 \left(\sum_{i=1}^n |p_{xi} - p_{yi}| \right)$, where p_{xi} is the mean $\%M$ of prey taxon i for season x and p_{yi} is the mean $\%M$ of prey taxon i for season y . The index varies from 0 (no overlap) to 1 (complete overlap; Guilbard *et al.*, 2007). Any fish with an empty stomach was excluded from stomach content analyses.

BODY TEMPERATURE (T_B)

Mean seasonal and interval body temperatures (T_B) of *S. fontinalis* were obtained from a concurrent tracking study using temperature–pressure sensor acoustic transmitters (V9TP and V13TP, Vemco/Amirix Ltd; www.vemco.com) and active (VR100) and passive receivers (VR2W and VR3-UWM), following the procedures outlined in the study of Spares *et al.* (2012). Simultaneous detections on multiple receivers and temperatures recorded beyond the transmitter's calibrated range and below saltwater freezing point (-1.9°C ; DeVries & Cheng, 2005) were omitted.

SEASONAL FEEDING INTENSITY

To estimate feeding activity between seasons, percentage of empty stomachs ($\%ES$) and indices for stomach fullness (I_R) and body condition factor (K) were calculated using all sampled fish (Rikardsen *et al.*, 2006), whereas means for number of prey, mass of prey (M_P), mass of vegetal and miscellaneous matter and consumption rate (C_{24} ; Richter *et al.*, 2004) were calculated from fish with prey or vegetal and miscellaneous matter present in their stomachs (Guilbard *et al.*, 2007). The degree of stomach fullness was calculated using Hureau's index (I_R), where $I_R = 1000 M_P M^{-1}$ [mg g^{-1} ; Tudela & Palomera (1995); McLean *et al.* (2013)]. Food consumption rate of *S. fontinalis* was estimated as the daily ration (C_{24} ; mg g^{-1}) using the Eggers method, so that $C_i = I_R R t + (I_{RT} - I_{RO})$, where C_i is the consumption over the feeding interval considered, I_R is the mean stomach fullness index for the interval, R is the instantaneous gastric evacuation rate (h^{-1}), t is the interval duration (h), I_{RO} is the mean stomach fullness

index at the beginning of the interval and I_{RT} is the mean stomach fullness index at the end of the interval (Amundsen & Klemetsen, 1988; Tudela & Palomera, 1995; Rikardsen *et al.*, 2006). Six feeding intervals were considered: 19 November to 13 December, 13 December to 7 January, 7 January to 29 January, 29 January to 4 March, 4 March to 8 April and 8 April to 5 May. Mean I_{RO} and I_{RT} values were calculated from samples captured within 24 h of the beginning and end dates. The rate of gastric evacuation of *S. fontinalis* and its relation to temperature was estimated by Sweka *et al.* (2004) in laboratory studies using fly and beetle larvae as prey, and these estimates were adopted for this study. Fulton's condition factor (K) was calculated using $K = 10^5 M L_F^{-3}$ (Ricker, 1975). A low K value (0.80) represented a fish in poor condition with a large head and narrow, thin body, whereas a large K value (1.60) indicated a fish in excellent condition with a well-proportioned, thick body, usually trophy class (Barnham & Baxter, 2003).

DATA ANALYSIS

Due to low sample sizes, a cumulative prey taxa abundance curve was generated by randomly ordering stomach samples to estimate the number of samples needed to compare taxa diversity between seasons. For all seasonal comparisons, either a parametric (ANOVA *post hoc* Tukey) or a non-parametric [Kruskal–Wallis with pair-wise comparisons using a Dwass–Steel–Critchlow–Fligner (D–S–C–F)] test was conducted, with normal and non-normal sample distribution (Shapiro–Wilk test) determining the test, respectively (Baran & Warry, 2008). Outliers were identified using box-and-whisker plots generated by Systat 13 software and removed for hypotheses testing (Systat; www.systat.com). Means for %O, %N and %M were generated. An α level of 0.05 was used for all tests.

RESULTS

FISH SAMPLING

Mean \pm s.d. L_F for all *S. fontinalis* sampled was 330 ± 70 mm ($n = 63$; Fig. 2). Mean \pm s.d. M was 462 ± 282 g ($n = 56$), with fish masses unmeasured in the field removed from any statistical analysis involving M . Minimum and maximum L_F and M of *S. fontinalis* captured in autumn and spring were 179 and 450 mm, and 42 and 1235 g (Table I), respectively. There was a significant increase in L_F and M from autumn to spring (L_F , ANOVA *post hoc* Tukey, $F = 4.93$, d.f. = 2, $P < 0.01$, $n = 63$; \sqrt{M} , $F = 7.545$, d.f. = 2, $P < 0.001$, $n = 56$; Fig. 3).

STOMACH CONTENT ANALYSIS

Stomach content diversity expressed as total n of taxa present was highest in spring ($n = 32$) with the median number of taxa highest in autumn [2 (3.3)] and lowest in winter [1 (0.8); Table I; Kruskal–Wallis *post hoc* D–S–C–F: $t = 6.76$, d.f. = 2, $P < 0.05$, five outliers removed]. The cumulative prey taxa abundance curve revealed the maximum number of taxa to be 34 for the entire sampling period, and minimum of five taxa during winter, reaching these sample size asymptotes within 52 and three stomachs, respectively (Fig. 4). Stomach content indices revealed fish as the dominant component, occurring in 90.6% of all stomachs containing prey, as 58.7% by number of items, 93.1% wet mass of contents and >85% O and >75% M throughout all seasons, with the highest %N (76.1%) occurring in spring. Fundulidae [mummichog *Fundulus heteroclitus* (L. 1766)], Atherinopsidae [Atlantic silverside *Menidia menidia* (L. 1766)] and Gasterosteidae [*Apeltes quadracus* (Mitchill 1815), *Gasterosteus aculeatus* L. 1758,

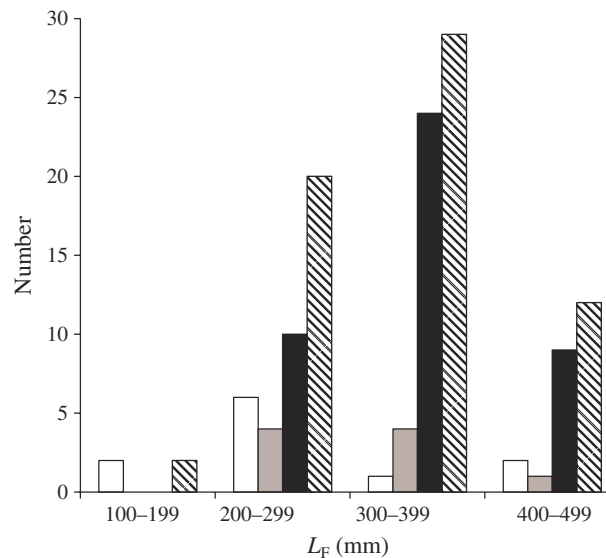


FIG. 2. Fork length (L_F) frequency of sea-run *Salvelinus fontinalis* captured during autumn ($n = 11$; □), winter ($n = 9$; ▒) and spring ($n = 43$; ■), and all data pooled ($n = 63$; ▨), from 2010 to 2012 in Antigonish Harbour, Nova Scotia, Canada.

Pungitius pungitius (L. 1758)] were consumed the most, constituting 14.4, 2.0 and 12.1 %N, and 69.3, 11.2 and 6.2 %M, respectively. Atherinopsidae only occurred in stomachs during winter and spring, constituting 10.0 %N and 22.9 %M of the winter diet (Table II and Fig. 5). Surprisingly, the largest prey item was an American eel *Anguilla rostrata* (LeSueur 1817) (220 mm total length, L_T , 22.8 g) coiled inside the stomach of a 448 mm L_F , 1235 g *S. fontinalis*. Seasonal specialities were Gammaridae in autumn (71.4 %O, 84.5 %N and 20.0 %M), Nereidae during winter (14.3 %O, 45.0 %N and 11.9 %M) and fish eggs in spring (2.6 %O, 42.1 %N and 0.2 %M; Fig. 5). Insects occurred during all seasons, and included 20 identified families, with caddis (Limnephilidae) and damsel (Coenagrionidae) flies, and ground (Carabidae) and scarab (Scarabaeidae) beetles consumed the most often (Table II).

For *S. fontinalis* > 250 mm L_F which contained prey ($n = 49$, 9% ES), piscivory accounted for 93.9 %O, 43.2 %N, 94.3 %M and 129.1% I_{RI} . Of the *S. fontinalis* < 250 mm L_F containing prey ($n = 7$, 22% ES), only one individual had consumed Fundulidae (14.3 %O, 0.3 %N, 18.5 %M and 2.7% I_{RI} ; Fig. 6). Stomach contents of these smaller *S. fontinalis* included estuarine (Crangonidae, Gammaridae and Nereidae) and freshwater (Carabidae, Corydalidae, Dytiscidae, Limnephilidae and Lumbricidae) prey. One individual (213 mm L_F) had consumed 298 unidentified fish eggs (0.7 g wet mass), but these were not considered as fish for this analysis.

Percentage I_{RI} revealed Fundulidae (45.8%), Gasterosteidae (4.8%), Gammaridae (4.0%) and Atherinopsidae (2.2%) as the most valuable prey items year-round, with Gammaridae most prevalent in autumn (74.6%) and Fundulidae in winter (41.3%) and spring (53.9%; Fig. 5). The Shannon–Weiner diversity index was highest in autumn (1.28) and lowest in spring (1.06) with complete overlap (1.00) between seasons indicated by Schoener's overlap index (Table I).

TABLE I. Seasonal comparison of fork length (L_F), body mass (M), diet diversity, body temperature (T_B), feeding intensity and body condition (K) indices for sea-run *Salvelinus fontinalis* captured in Antigonish Harbour, Nova Scotia, Canada, during 2010–2012. Outliers were removed for all calculations, minimum and maximum values are given in parentheses

| | Autumn | Winter | Spring | All |
|---|---------------------------------|---------------------------------|---------------------------------|---------------------------------|
| Mean \pm S.D. L_F (mm) | 278 \pm 89 (179, 443) | 317 \pm 48 (256, 410) | 346 \pm 62 (213, 450) | 330 \pm 70 (179, 450) |
| n | 11 | 9 | 43 | 63 |
| Mean \pm S.D. M (g) | 270 \pm 303 (42, 965) | 363 \pm 189 (140, 740) | 540 \pm 262 (150, 1235) | 462 \pm 282 (42, 1235) |
| n | 11 | 8 | 37 | 56 |
| Total n taxa | 13 | 5 | 32 | 34 |
| Median n taxa | 2, 3.3 (1, 6) | 1, 0.8 (1, 3) | 1, 1 (1, 15) | 1, 1 (1, 15) |
| n | 9 | 7 | 40 | 56 |
| H' | 1.28 | 1.12 | 1.06 | 1.17 |
| I_S | | 1.00 | 1.00 | |
| Mean \pm S.D. T_B ($^{\circ}$ C) | 8.6 \pm 3.6 (1.3, 20.1) | 0.7 \pm 1.2 (-0.5, 4.7) | 9.0 \pm 3.4 (0.2, 19.3) | 7.6 \pm 4.4 (-0.5, 20.1) |
| n | 1147 | 9548 | 45 547 | 56 242 |
| n with prey | 9 | 7 | 40 | 56 |
| n empty | 2 | 2 | 3 | 7 |
| % Empty stomachs | 18 | 22 | 7 | 11 |
| Median n prey | 4, 4.5 (1, 10) | 5, 4 (2, 18) | 5, 9.8 (1, 28) | 5, 8 (1, 28) |
| n | 7 | 6 | 37 | 50 |
| Median total prey mass (g) | 0.44, 2.49 (0.001, 3.94) | 14.00, 9.16 (1.25, 17.21) | 5.37, 11.77 (0.05, 24.69) | 4.78, 12.39 (0.001, 24.69) |
| n | 8 | 7 | 40 | 55 |
| n with vegetal and miscellaneous matter | 3 | 3 | 8 | 14 |
| Median mass of vegetal and miscellaneous matter (g) | 0.09, 0.10 (0.05, 0.14) | 0.30, 0.30 (0.11, 0.50) | 0.09, 0.11 (0.04, 0.38) | 0.11, 0.17 (0.04, 0.50) |
| n | 2 | 3 | 7 | 12 |
| Median I_R (mg g^{-1})* | 0.6, 3.5 (0, 17.5) | 22.2, 43.0 (0, 60.8) | 12.7, 16.4 (0, 43.8) | 11.5, 18.6 (0, 68.2) |
| n | 9 | 8 | 36 | 53 |
| Mean \pm S.D. K | 0.90 \pm 0.12 (0.73, 1.11) | 1.10 \pm 0.16 (0.82, 1.25) | 1.31 \pm 0.15 (0.98, 1.61) | 1.20 \pm 0.22 (0.73, 1.61) |
| n | 11 | 8 | 37 | 56 |

H' , Shannon–Weiner index; I_S , Schoener's overlap index; I_R , stomach fullness.

*Includes empty stomachs.

BODY TEMPERATURE (T_B)

There was a significant difference between mean \pm S.D. body temperatures of *S. fontinalis* for each season (ANOVA *post hoc* Tukey, $F = 27\ 445$, d.f. = 2, $P < 0.000$), calculated as 8.6 \pm 3.6 $^{\circ}$ C ($n = 1147$) during autumn, 0.7 \pm 1.2 $^{\circ}$ C ($n = 9548$) in winter and 9.0 \pm 3.4 $^{\circ}$ C ($n = 45\ 547$) in spring, with an overall T_B of 7.6 \pm 4.4 $^{\circ}$ C (minimum = -0.5 $^{\circ}$ C, maximum = 20.1 $^{\circ}$ C, $n = 56\ 242$; Table I).

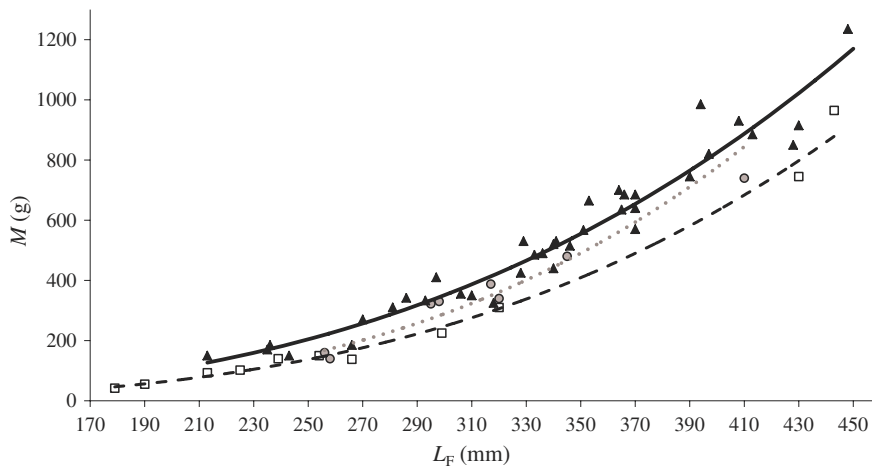


FIG. 3. Mass (M) and fork length (L_F) relationships for sea-run *Salvelinus fontinalis* ($n = 63$) captured from 2010 to 2012 during autumn (19 November to 13 December; \square , ---; $y = 2E-06x^{3.24}$; $r^2 = 0.988$, $n = 11$), winter (7 January to 5 March; \circ ,; $y = 9E-07x^{3.43}$; $r^2 = 0.938$, $n = 9$) and spring (5 April to 5 May; \blacktriangle , —; $y = 2E-05x^{2.97}$; $r^2 = 0.954$, $n = 43$).

FEEDING INTENSITY

Prey occurred in 56 of all *S. fontinalis* stomachs sampled: nine in autumn, seven in winter and 40 in spring. Percentage of empty stomachs was high during autumn (18%) and winter (22%) and lowest in spring (7%). The median number of prey per stomach did not change significantly with the seasons [four to five (4.0–9.8), Kruskal–Wallis test, $t = 0.868$, d.f. = 2, $P > 0.05$, $n = 50$, six outliers removed], whereas median M_P

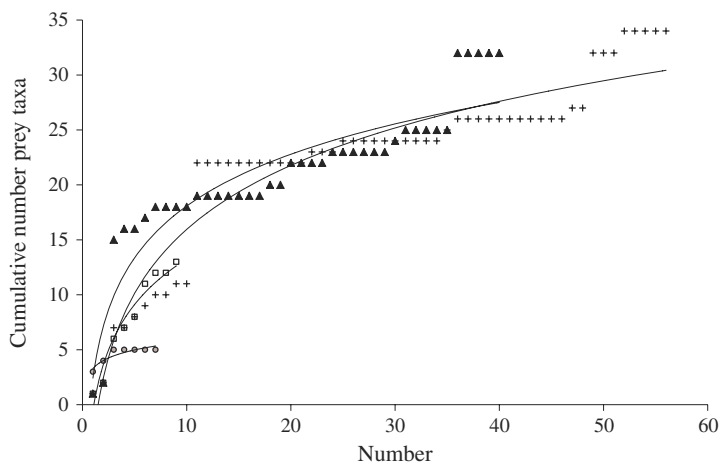


FIG. 4. Cumulative number of prey taxa for sea-run *Salvelinus fontinalis* containing prey during 2010 to 2012 ($n = 56$; +), autumn (19 November to 13 December; $n = 9$; \square), winter (7 January to 5 March; $n = 7$; \circ) and spring (5 April to 5 May; $n = 40$; \blacktriangle) with trend line asymptotes showing minimum sample size needed to reach maximum number of taxa.

TABLE II. Summary of stomach contents of *Salvelinus fontinalis* ($n = 63$) captured from November to May 2010–2012, in Antigonish Harbour, Nova Scotia, Canada. Indices used are frequency of occurrence (%O), per cent by number (%N) and per cent by mass (%M). Frequency of occurrence is expressed relative to the total number of stomachs containing food ($n = 53$)

| <i>n</i> | %O | | | | %N | | | | %M | | | |
|-------------------------------|------|--------|--------|--------|------|--------|--------|--------|------|--------|--------|--------|
| | All | Autumn | Winter | Spring | All | Autumn | Winter | Spring | All | Autumn | Winter | Spring |
| Estuarine prey items | 53 | 7 | 7 | 39 | 63 | 11 | 9 | 43 | 63 | 11 | 9 | 43 |
| Actinopterygii | 90.6 | 85.7 | 100.0 | 89.7 | 58.7 | 8.8 | 53.8 | 76.1 | 93.1 | 75.3 | 86.9 | 95.6 |
| Anguillidae (freshwater eels) | 1.9 | 0.0 | 0.0 | 2.6 | 0.1 | 0.0 | 0.0 | 0.1 | 5.2 | 0.0 | 0.0 | 6.7 |
| Atherinopsidae (silversides) | 17.0 | 0.0 | 14.3 | 20.5 | 2.0 | 0.0 | 10.0 | 1.8 | 11.2 | 0.0 | 22.9 | 9.3 |
| Fundulidae (killifishes) | 54.7 | 28.6 | 57.1 | 59.0 | 14.4 | 3.4 | 16.3 | 18.0 | 69.3 | 51.4 | 56.0 | 73.4 |
| Gasterosteidae (sticklebacks) | 26.4 | 28.6 | 42.9 | 23.1 | 12.1 | 3.8 | 27.5 | 13.2 | 6.2 | 21.5 | 8.0 | 4.8 |
| Unidentified fish eggs | 1.9 | 0.0 | 0.0 | 2.6 | 29.1 | 0.0 | 0.0 | 42.1 | 0.2 | 0.0 | 0.0 | 0.2 |
| Unidentified fish remains | 17.0 | 28.6 | 0.0 | 17.9 | 1.3 | 1.7 | 0.0 | 1.3 | 1.1 | 2.4 | 0.0 | 1.2 |
| Crangonidae (sand shrimps) | 9.4 | 0.0 | 0.0 | 12.8 | 1.0 | 0.0 | 0.0 | 1.4 | 1.0 | 0.0 | 0.0 | 1.3 |
| Gammaridae (amphipods) | 17.0 | 71.4 | 0.0 | 10.3 | 22.7 | 84.5 | 0.0 | 4.5 | 1.1 | 20.0 | 0.0 | 0.2 |
| Nereidae (sandworms) | 5.7 | 0.0 | 14.3 | 5.1 | 4.5 | 0.0 | 45.0 | 1.4 | 3.0 | 0.0 | 11.9 | 1.3 |
| Freshwater prey items | | | | | | | | | | | | |
| Amnicolida (aquatic snails) | 1.9 | 14.3 | 0.0 | 0.0 | 0.2 | 0.8 | 0.0 | 0.0 | 0.0 | 0.1 | 0.0 | 0.0 |
| Lumbricidae (earthworms) | 1.9 | 0.0 | 0.0 | 2.6 | 0.2 | 0.0 | 0.0 | 0.3 | 0.3 | 0.0 | 0.0 | 0.4 |
| Insecta (insects) | 18.9 | 71.4 | 14.3 | 10.3 | 12.7 | 5.9 | 1.3 | 16.3 | 1.0 | 3.7 | 0.1 | 1.0 |
| Coenagrionidae (damselflies) | 5.7 | 14.3 | 0.0 | 5.1 | 1.9 | 0.4 | 0.0 | 2.5 | 0.1 | 0.3 | 0.0 | 0.2 |
| Cicadellidae (leafhoppers) | 3.8 | 0.0 | 0.0 | 5.1 | 0.3 | 0.0 | 0.0 | 0.4 | 0.0 | 0.0 | 0.0 | 0.0 |
| Formicidae (flying ants) | 3.8 | 0.0 | 0.0 | 5.1 | 0.3 | 0.0 | 0.0 | 0.4 | 0.0 | 0.0 | 0.0 | 0.0 |
| Apidae (honeybees) | 3.8 | 0.0 | 0.0 | 5.1 | 0.1 | 0.0 | 0.0 | 0.1 | 0.0 | 0.0 | 0.0 | 0.0 |
| Coleoptera (beetles) | 9.4 | 42.9 | 0.0 | 5.1 | 8.7 | 2.5 | 0.0 | 11.7 | 0.6 | 1.6 | 0.0 | 0.7 |
| Carabidae (ground) | 5.7 | 14.3 | 0.0 | 5.1 | 3.1 | 0.4 | 0.0 | 4.4 | 0.2 | 0.0 | 0.0 | 0.3 |
| Dytiscidae (diving) | 1.9 | 14.3 | 0.0 | 0.0 | 0.3 | 1.3 | 0.0 | 0.0 | 0.1 | 1.1 | 0.0 | 0.0 |
| Staphylinidae (rove) | 3.8 | 0.0 | 0.0 | 5.1 | 3.0 | 0.0 | 0.0 | 4.4 | 0.2 | 0.0 | 0.0 | 0.2 |

TABLE II. Continued

| | %O | | | %N | | | %M | | | | | |
|-----------------------------|------|--------|--------|--------|-----|--------|--------|--------|-----|--------|--------|--------|
| | All | Autumn | Winter | Spring | All | Autumn | Winter | Spring | All | Autumn | Winter | Spring |
| Elateridae (click) | 3.8 | 0.0 | 0.0 | 5.1 | 0.5 | 0.0 | 0.0 | 0.7 | 0.1 | 0.0 | 0.0 | 0.1 |
| Scarabaeidae (scarab) | 5.7 | 14.3 | 0.0 | 5.1 | 0.6 | 0.4 | 0.0 | 0.7 | 0.0 | 0.2 | 0.0 | 0.0 |
| Hydrophilidae (water) | 3.8 | 14.3 | 0.0 | 2.6 | 0.2 | 0.4 | 0.0 | 0.1 | 0.0 | 0.3 | 0.0 | 0.0 |
| Curculionidae (weevils) | 3.8 | 0.0 | 0.0 | 5.1 | 0.2 | 0.0 | 0.0 | 0.3 | 0.0 | 0.0 | 0.0 | 0.1 |
| Chrysomelidae (leaf) | 1.9 | 0.0 | 0.0 | 2.6 | 0.1 | 0.0 | 0.0 | 0.1 | 0.0 | 0.0 | 0.0 | 0.0 |
| Coccinellidae (ladybugs) | 1.9 | 0.0 | 0.0 | 2.6 | 0.1 | 0.0 | 0.0 | 0.1 | 0.0 | 0.0 | 0.0 | 0.0 |
| Pentatomidae (stinkbugs) | 1.9 | 0.0 | 0.0 | 2.6 | 0.1 | 0.0 | 0.0 | 0.1 | 0.0 | 0.0 | 0.0 | 0.0 |
| Cydnidae (burrower bugs) | 3.8 | 0.0 | 0.0 | 5.1 | 0.6 | 0.0 | 0.0 | 0.8 | 0.0 | 0.0 | 0.0 | 0.0 |
| Corydalidae (fishflies) | 1.9 | 14.3 | 0.0 | 0.0 | 0.2 | 0.8 | 0.0 | 0.0 | 0.0 | 0.8 | 0.0 | 0.0 |
| Calliphoridae (blowflies) | 1.9 | 0.0 | 0.0 | 2.6 | 0.1 | 0.0 | 0.0 | 0.1 | 0.0 | 0.0 | 0.0 | 0.0 |
| Limnephilidae (caddisflies) | 5.7 | 28.6 | 14.3 | 0.0 | 0.3 | 0.8 | 1.3 | 0.0 | 0.0 | 0.6 | 0.1 | 0.0 |
| Leptophlebitidae (mayflies) | 1.9 | 0.0 | 0.0 | 2.6 | 0.3 | 0.0 | 0.0 | 0.4 | 0.0 | 0.0 | 0.0 | 0.0 |
| Acrididae (grasshoppers) | 1.9 | 0.0 | 0.0 | 2.6 | 0.1 | 0.0 | 0.0 | 0.1 | 0.0 | 0.0 | 0.0 | 0.0 |
| Unidentified insect remains | 7.5 | 42.9 | 0.0 | 2.6 | 0.4 | 1.3 | 0.0 | 0.1 | 0.0 | 0.3 | 0.0 | 0.0 |
| Araneae (spiders) | 1.9 | 0.0 | 0.0 | 2.6 | 0.1 | 0.0 | 0.0 | 0.1 | 0.0 | 0.0 | 0.0 | 0.0 |
| Unidentified/miscellaneous | 26.4 | 42.9 | 42.9 | 20.5 | — | — | — | — | 0.9 | 7.0 | 1.2 | 0.5 |

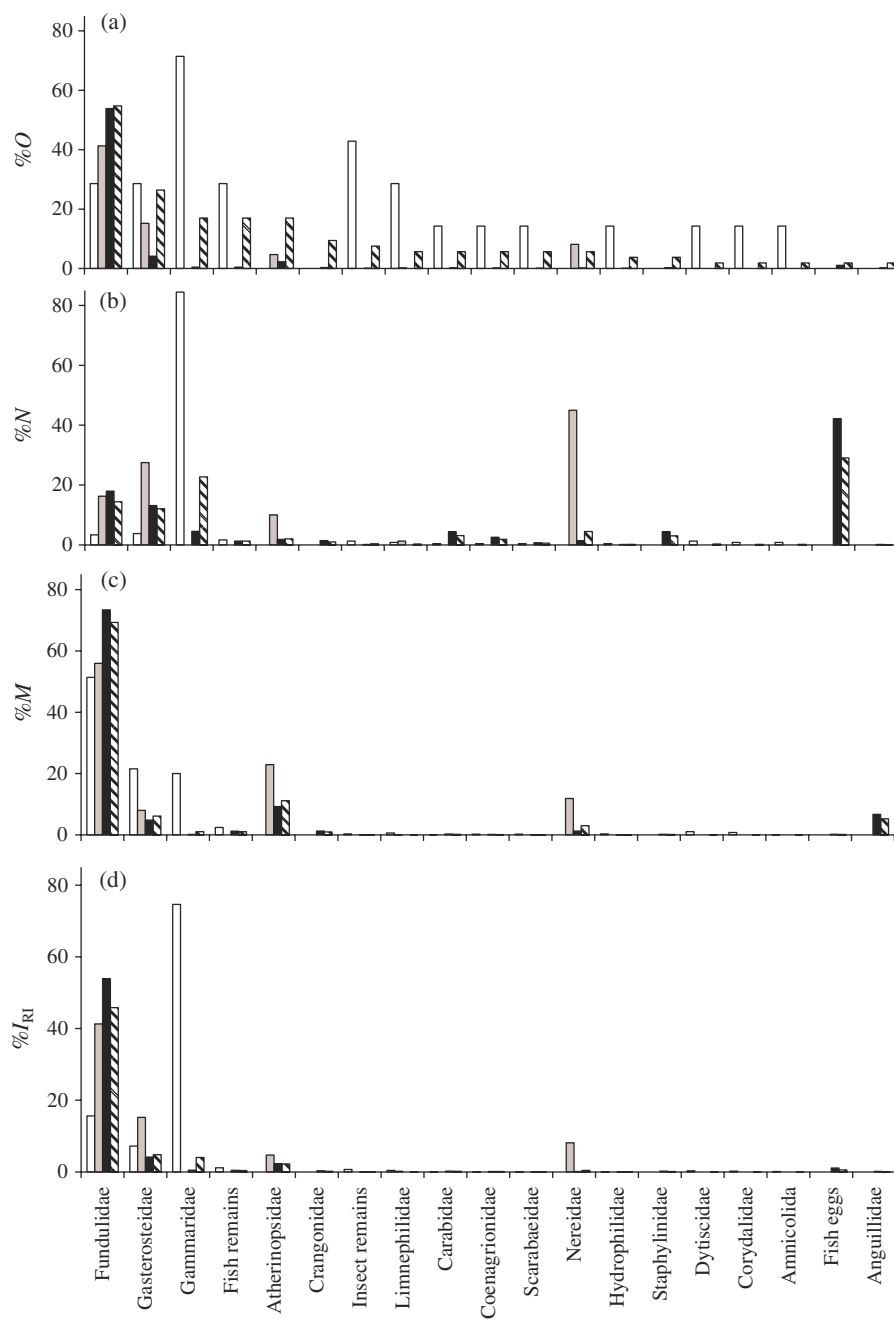


FIG. 5. (a) Relative per cent occurrence (%O), (b) abundance (%N) and (c) mass (%M) of taxa collected from the stomach contents of sea-run *Salvelinus fontinalis* ($n = 56$) captured during autumn (\square), winter (\square) and spring (\blacksquare), and all data pooled (\blacksquare), from 2010 to 2012 in Antigonish Harbour, Nova Scotia, Canada. (d) The per cent index of relative importance (%IRI) of each taxa to *S. fontinalis* diet is also presented. Prey taxa with %O < 10 were not included but the following order (Araneae) and families: Acrididae, Apidae, Calliphoridae, Chrysomelidae, Cicadellidae, Coccinellidae, Curculionidae, Cydnidae, Elateridae, Formicidae, Leptophlebiidae, Lumbricidae and Pentatomidae were recovered.

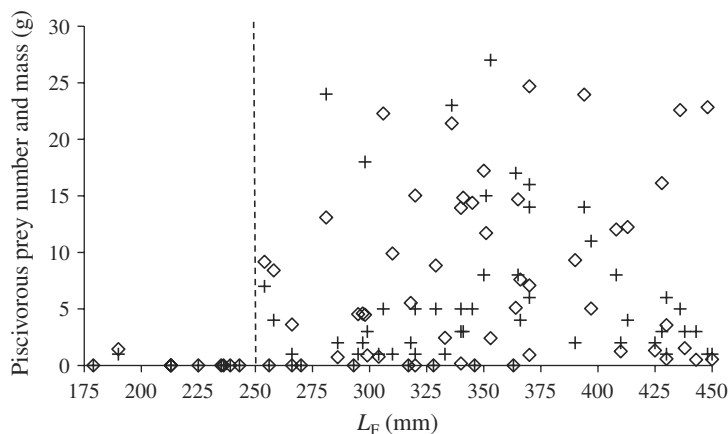


FIG. 6. Fork length (L_F) and piscivory shown by number (+) and wet mass (◇) of fishes consumed by sea-run *Salvelinus fontinalis* captured in Antigonish Harbour, Nova Scotia, Canada, from November to May 2010–2012.

was significantly higher in winter [14.00 g (9.16), $n = 7$], compared to spring [5.37 (11.77), $n = 40$], and autumn [0.44 (2.49), $n = 8$, one outlier removed; Kruskal–Wallis *post hoc* D-S-C-F, $t = 11.76$, d.f. = 2, $P < 0.05$]. The percentage of stomachs containing vegetal and miscellaneous matter was highest in winter (43%) and lowest in spring (20%) with no significant seasonal difference in median vegetal mass (Kruskal–Wallis test, $t = 2.89$, d.f. = 2, $P > 0.05$, two outliers removed; Table I).

There were significant seasonal differences (Kruskal–Wallis *post hoc* D-S-C-F, $t = 8.30$, d.f. = 2, $P \leq 0.02$) in I_R with the lowest median index of 0.6 in autumn [(interquartile range = 3.5), $n = 9$, two outliers removed], 12.7 during spring [(16.4), $n = 36$, one outlier removed] and highest of 22.2 in winter [(43.0), $n = 8$; Table I]. Further divisions into approximately monthly intervals (28 ± 5 days) revealed mean stomach fullness indices following a similar pattern (Fig. 7), beginning at a mean \pm s.d. of 11.6 ± 21.3 from 19 November to 13 December, increasing to a maximum of 32.6 ± 24.7 from 29 January to 4 March and decreasing to 11.7 ± 11.5 from 4 March to 8 April (Table III). Estimates of consumption rate (C_{24}) revealed a reciprocal relationship (Fig. 7) with the highest values of 3.67 and 5.93 mg g⁻¹ occurring during 19 November to 13 December and 8 April to 5 May, respectively, and negative consumption values occurring from 7 January to the 4 March (Fig. 7). Negative consumption corresponded to recorded body temperatures of -0.5 to 3.8° C (Table III).

Mean \pm s.d. K of *S. fontinalis* increased significantly from 0.90 ± 0.12 in autumn ($n = 11$) to 1.10 ± 0.16 in winter ($n = 8$), and peaked at 1.31 ± 0.15 ($n = 37$) in spring (Table I and Fig. 8; $r^2 = 0.577$, $n = 56$; ANOVA *post hoc* Tukey, $F = 34.63$, d.f. = 2, $P < 0.05$). Minimum and maximum K indices of 0.73 and 1.61 occurred during autumn and spring, respectively (Table I).

DISCUSSION

Salmonid populations feeding in marine environments have demonstrated differences in energy allocation to somatic growth, body maintenance, gonad development and

TABLE III. Summary of calculations (mean \pm s.d.; minimum and maximum in parentheses) used to estimate consumption rates (C_{24}) of sea-run *Salvelinus fontinalis* during seasonal intervals from 19 November to 5 May 2010–2012, in Antigonish Harbour, Nova Scotia, Canada. Calculations include body temperature (T_B), stomach fullness at beginning of interval (I_{RO}), stomach fullness at end of interval (I_{RT}), stomach fullness over entire interval (I_R), instantaneous gastric evacuation rate [R , estimated from Sweka *et al.* (2004)] and interval duration (t)

| Interval | 19 November to 13 December | 13 December to 7 January | 7 January to 29 January | 29 January to 4 March | 4 March to 8 April | 8 April to 5 May |
|--------------------------|---------------------------------|------------------------------|---------------------------------|---------------------------------|-------------------------------|--------------------------------|
| T_B ($^{\circ}$ C) | 6.3 \pm 1.7 (3.0, 9.1) | 3.9 \pm 1.6 (0.5, 9.4) | 1.4 \pm 1.3 (0.02, 3.8) | 0.1 \pm 0.2 (-0.5, 2.1) | 3.5 \pm 2.6 (-0.1, 11.5) | 7.4 \pm 2.5 (0.7, 14.9) |
| n | 413 | 754 | 2208 | 5564 | 7158 | 23 108 |
| I_{RO} (mg g $^{-1}$) | 1.22 \pm 1.71 (0.00, 2.43) | 18.3 \pm 29.0 (0, 68.6) | 15.0 \pm 21.2 (0, 30.0) | 52.5 \pm 11.8 (44.2, 60.8) | 19.3 \pm 22.1 (0, 43.5) | 10.3 \pm 6.4 (2.6, 21.9) |
| n | 2 | 5 | 2 | 2 | 3 | 9 |
| I_{RT} (mg g $^{-1}$) | 18.3 \pm 29.0 (0, 68.6) | 15.0 \pm 21.2 (0, 30.0) | 52.5 \pm 11.8 (44.2, 60.8) | 19.3 \pm 22.1 (0, 43.5) | 10.3 \pm 6.4 (2.6, 21.9) | 27.8 \pm 12.4 (6.2, 43.8) |
| n | 5 | 2 | 2 | 3 | 9 | 9 |
| I_R (mg g $^{-1}$) | 11.6 \pm 21.3 (0, 68.6) | 17.3 \pm 25.3 (0, 68.6) | 27.3 \pm 26.5 (0, 60.8) | 32.6 \pm 24.7 (0, 60.8) | 11.7 \pm 11.5 (0, 43.5) | 16.1 \pm 14.1 (0, 62.8) |
| n | 11 | 7 | 5 | 5 | 13 | 36 |
| R | 0.0106 | 0.0047 | -0.0090 | -0.0217 | 0.0031 | 0.0120 |
| t (h) | 576 | 600 | 528 | 816 | 840 | 648 |
| C_{24} (mg g $^{-1}$) | 3.67 | 1.89 | -3.85 | -25.4 | 0.90 | 5.93 |

n , sample size.

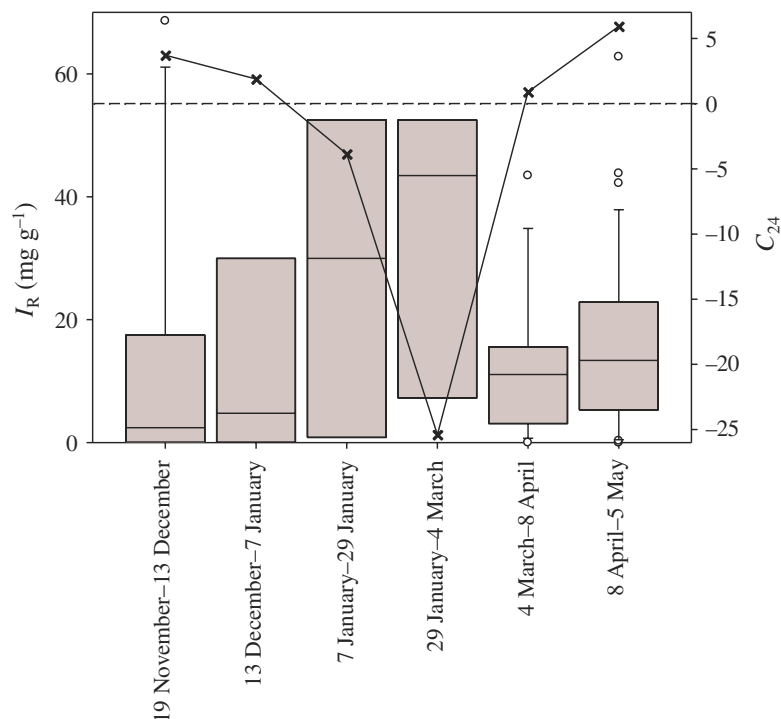


FIG. 7. Relationship between stomach fullness indices (I_R ; \square) and daily consumption rates (C_{24} ; \times), calculated for sea-run *Salvelinus fontinalis* captured within intervals from 19 November to 5 May 2010–2012, in Antigonish Harbour, Nova Scotia, Canada. \circ , I_R outliers.

lipid deposition (Rikardsen, 2004; Olsen *et al.*, 2006; Rikardsen *et al.*, 2006). Considering members of the genus *Salvelinus* display a high degree of life-history variability, with anadromous populations exhibiting irregular periods of marine residence (Brenkman *et al.*, 2007), it is unclear which of these strategies is more common for *S. fontinalis*. *Salvelinus fontinalis* feeding in Antigonish Harbour from autumn to spring appear to channel energy gained into somatic growth. An individual (258 mm L_F) tagged on 7 April in Antigonish Harbour was recaptured on 14 June in the Wrights River, and revealed an L_F increase of 47 mm in 68 days (unpubl. data), lending evidence for rapid somatic growth. Significant increases in body mass and condition from autumn to spring, however, also suggested allocation to lipid deposition. More detailed studies would be needed to determine if energy allocation changes with ontogeny and season (Olsen *et al.*, 2006).

SEASONAL DIET

Amphipods have been a dominant food item during *Salvelinus* spp. marine migrations (Gaudreault *et al.*, 1982; Morinville & Rasmussen, 2006; Spares *et al.*, 2012). Gaudreault *et al.* (1982) found crustaceans (75% Gammaridae and 25% Mysidacea) to occur in *S. fontinalis*'s diet throughout their entire marine migration in the St-Jean Estuary, Québec, consuming the most during January to February (75.0 %O and 94.7 %N).

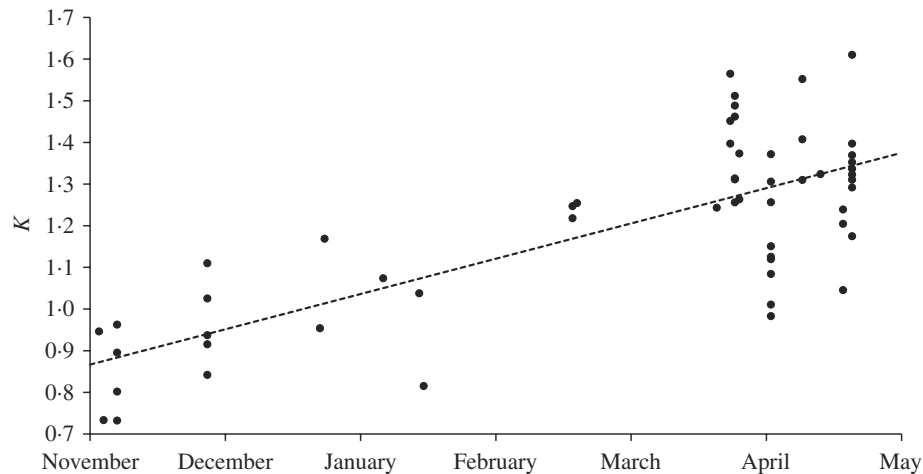


Fig. 8. Body condition factor (K) of sea-run *Salvelinus fontinalis* captured in Antigonish Harbour, Nova Scotia, Canada, from November to May 2010–2012 ($y = 0.0032x - 129.87$; $r^2 = 0.536$, $n = 63$).

In contrast, Antigonish Harbour migrants consumed no Gammaridae during winter, and the most during autumn (71.4% O , 84.5% N and 74.6% I_{RI}). Migrants in the Matamek River estuary, Québec, similarly consumed amphipods the most from late-August to early October (Whoriskey *et al.*, 1981). Considering amphipods breed during summer (Ruppert & Barnes, 1994), their increased abundance during late-summer and autumn due to recruitment was probably taken advantage of by feeding *S. fontinalis*.

Nereidae were considered a major winter diet component (14.3% O , 45.0% N and 11.9% M) of Antigonish Harbour *S. fontinalis*, but analyses were based on nine *S. fontinalis*, with one consuming 36 *Nereis* sp. and one *Fundulus* sp., thus, possibly misrepresenting the importance of Nereidae. Gaudreault *et al.* (1982) found winter polychaete predation to be considerably lower (7.1% O and 1.5% N , $n = 28$). Occurrence of Nereidae in this study coincided with the highest percentage of vegetal and miscellaneous matter in stomachs (43%), suggesting *S. fontinalis* were cued to benthic feeding. Cueing on nekto-benthic and benthic prey during winter, mainly crustaceans and polychaetes, has been observed in other *S. fontinalis* (Gaudreault *et al.*, 1982) and *S. trutta* (Pemberton, 1976; Rikardsen *et al.*, 2006) populations. Morinville & Rasmussen (2006) noted polychaetes as a dominant prey of *S. fontinalis* remaining near freshwater inputs of St Marguerite Bay, and suggested that estuarine fidelity minimized osmoregulation costs. This may be the case for Antigonish Harbour *S. fontinalis*, as most of them were captured during winter in the estuary of the West River where mean \pm s.d. salinities and water temperatures were 4.5 ± 6.9 (minimum = 0.1, maximum = 21.5; $n = 57$) and $1.0 \pm 1.4^\circ$ C (minimum = -0.1° C, maximum = 6.1° C; $n = 57$), respectively (unpubl. data). Ice fishers provided information on observations of *S. fontinalis* feeding on polychaetes in shallow water (depth < 1 m) near the main river channel during February and March. This was further supported by sea-run *S. trutta*, caught concurrently with *S. fontinalis*, regurgitating *Nereis* sp. only (A. D. Spares, pers. obs.). Whether or not the present results accurately estimate the contribution of Nereidae to Antigonish Harbour *S. fontinalis* winter diet, the fact that Nereidae do not occur

as prey in autumn, and are more important in winter compared to spring, suggests a seasonal specialization.

Insects occurred as prey during the entire sampling period and included 20 taxa, but their occurrence was limited to a few stomachs. For example, two *S. fontinalis* captured in spring had consumed 13 and 15 taxa, of which 11 (85%) and 14 (93%), respectively, were insects. Most insect prey during spring were Carabidae and Scarabaeidae, probably taken as surface prey (Rikardsen *et al.*, 2006) considering terrestrial ecosystems virtually enclose Antigonish Harbour (Fig. 1). Aquatic insect prey occurred in all seasons, which suggested individuals had returned to fresh water briefly, or had re-entered salt water from an extended freshwater stay. The caddisfly tube found in an individual captured on 5 March may have been undigested and unevacuated for weeks considering cold water temperatures and the tube's sand grain composition (A. D. Spares, pers. obs.). Gaudreault *et al.* (1982) found Ephemeroptera larvae and Trichoptera during January to February in *S. fontinalis* stomachs, which suggested migrants were foraging near freshwater inputs. Aquatic insects occurring in early May samples also suggests that individuals may have re-entered fresh water temporarily before their main re-entry during mid-May to mid-June for summer and autumn residency (unpubl. data). The occurrence of aquatic insects from autumn to spring may suggest site-fidelity to freshwater inputs (Spares *et al.*, 2012).

Prey diversity, indicated by n of taxa consumed by migrants, varied considerably between a winter minimum ($n = 5$) and spring maximum ($n = 32$). This relative diet difference probably related to increased terrestrial insect activity in spring, which increased abundance of optimally sized prey items (Morinville & Rasmussen, 2006). The median n of taxa consumed per stomach remained the same throughout all seasons.

In fresh water, salmonids must often attain a size of 150–250 mm to show piscivory; however, this minimum size threshold varies by species. *Salmo trutta*, *S. fontinalis*, bull trout *Salvelinus confluentus* (Suckley 1859), cutthroat trout *Oncorhynchus clarki* (Richardson 1836) and sockeye salmon *Oncorhynchus nerka* (Walbaum 1792) have been shown to employ piscivory at $L_F > 200$ mm (Ibbotson *et al.*, 1996; Moyle, 2002; Nowak *et al.*, 2004; Miller *et al.*, 2007; Browne & Rasmussen, 2009). Piscivory, however, has been observed in an individual *S. trutta* as small as 85 mm L_F (Sánchez-Hernández *et al.*, 2012). *Salmo salar* smolts at $L_F < 150$ mm have been documented feeding extensively on fish larvae upon sea entry, suggesting prey type and availability influence piscivorous behaviour (Rikardsen & Dempson, 2011).

The present results concur with the general rule that anadromous *S. fontinalis* > 250 mm L_F show piscivory (Dutil & Power, 1980; Whoriskey *et al.*, 1981; Gaudreault *et al.*, 1982; O'Connell, 1982; Morinville & Rasmussen, 2006). The few *S. fontinalis* Gaudreault *et al.* (1982) found feeding on fish in the upper St-Jean Estuary during winter had focused on Gasterosteidae (75% *Pungitius* sp. and 25% *Gasterosteus* sp.), yet more *S. fontinalis* switched to piscivory during spring (May to June), adding *Ammodytes* sp. and *Osmerus* sp., and had fishes dominating diets by summer as migrants moved into the lower estuary (July to August; 45.5% *O* and 50% *N*). St Marguerite Bay *S. fontinalis* preyed almost entirely on *Osmerus* sp. in the upper Saguenay River from winter to spring, but diversified to also include Fundulidae, *Ammodytes* sp. and Gasterosteidae in St Marguerite Bay from May to September (Morinville & Rasmussen, 2006). Acoustic tracking and stomach content analysis of *S. fontinalis* in Sheet Harbour, Nova Scotia, revealed migrants remained around

shoals to feed on spring-spawned Atlantic herring larvae *Clupea harengus* L. 1758 (E. A. Halfyard, pers. comm.). Antigonish Harbour *S. fontinalis* followed a similar pattern, focusing almost entirely on Fundulidae and Gasterosteidae from autumn to spring in the inner harbour, but demonstrated seasonal diet changes to include Atherinopsidae during winter and spring and Anguillidae during spring. *Menidia menidia* occurred only during winter and spring, agreeing with their overwintering under estuarine sea ice (Needler, 1940) and spawning in spring (Scott & Scott, 1988). Antigonish Harbour *S. fontinalis* appear to use piscivory as their dominant feeding strategy, and similar to other populations (Dutil & Power, 1980; Whoriskey *et al.*, 1981; Gaudreault *et al.*, 1982; O'Connell, 1982; Morinville & Rasmussen, 2006) appear to focus on one or two prey types depending on habitat or season.

The Shannon–Weiner diversity index (H') was similar to stomach content analysis results, being the highest in autumn (1.28) and lowest in spring (1.06), which suggested that fish foraged on multiple taxa, with relative differences possibly relating to *S. fontinalis* feeding on both freshwater and saltwater prey during their return from rivers to the harbour in autumn, and their increasing preference for Fundulidae and Gasterosteidae fishes over the entire estuarine residency relating to the lowest diversity in spring. High preference for a few fishes during the entire migration is further indicated by complete seasonal diet overlap using Schoener's overlap index. Decreasing H' from autumn to spring seemingly contradicts the total number of taxa present within seasonal samples, which showed the lowest diversity of prey during winter and highest in spring, but H' is largely calculated using % M , which further reinforces the importance of a few taxa in Antigonish Harbour *S. fontinalis* diet.

SEASONAL FEEDING INTENSITY

All season samples of Antigonish Harbour *S. fontinalis* had some empty stomachs (<22% ES) similar to actively feeding *S. fontinalis* during winter in the upper Saguenay River, Québec (<20% ES; Morinville & Rasmussen, 2006). Indeed, none of the seasonal or overall % ES were even close to *S. fontinalis* which had ceased feeding (>75% ES; Morinville & Rasmussen, 2006). Higher occurrence of empty stomachs in autumn (18%) and winter (22%) compared to spring (7%), however, suggested that fish may have been having difficulty in feeding during autumn and winter. It should be noted that low sample sizes for autumn and winter may have misrepresented actual percentages. The present results agreed with sea-run *S. trutta* which showed that stomach fullness and feeding rates were lowest in autumn, along with a high percentage of empty stomachs (45–48%; Rikardsen *et al.*, 2006).

The lowest median M of prey and median stomach fullness index of Antigonish Harbour *S. fontinalis* during autumn indicates a low feeding intensity. Gaudreault *et al.* (1982) suggested that the low mean stomach fullness index for *S. fontinalis* captured in fresh water was due to low prey availability. This may suggest that some Antigonish Harbour *S. fontinalis* had recently re-entered salt water from fresh water during autumn and were experiencing difficulty in obtaining prey. Mean stomach fullness indices were virtually the same for autumn (11.6 mg g⁻¹) and spring (11.7 mg g⁻¹), suggesting similar feeding intensities. Autumn and spring indices were comparable to indices (16.7–18.1 mg g⁻¹) for *S. fontinalis* feeding in the St-Jean Estuary from winter to summer (Gaudreault *et al.*, 1982). The difference between autumn median and mean stomach fullness indices for Antigonish Harbour *S. fontinalis* was associated with a low

sample size, yet the spread of data agreed with individuals exhibiting varying degrees of feeding intensity at the beginning of their marine migration.

The present winter results appear to suggest that feeding intensity peaked with the highest median prey M and median and mean stomach fullness indices, but these results were contradicted by the highest % ES and negative consumption rates. Other *S. fontinalis* seasonal feeding studies have found higher M_p in winter (Elliott & Jenkins, 1972) and similar stomach fullness indices in winter and summer (Gaudreault *et al.*, 1982). No mid-winter sampling was conducted by Rikardsen *et al.* (2006); however, consumption rates for *S. trutta* were decreasing from November to December and increasing from March to April, which suggests a minimum consumption rate during mid-winter (January to February) when temperatures approached 1° C (Rikardsen, 2004). This appeared to be the case in this study where negative consumption rates corresponded to the coldest *S. fontinalis* body temperatures, which may have essentially lowered feeding (Power, 1980) and decreased digestion to ineffective rates (Gaudreault *et al.*, 1982; Sweka *et al.*, 2004).

Gastric evacuation periods of *S. fontinalis* indicate that 1 week is needed to empty a full stomach at 4° C (Sweka *et al.*, 2004). Comparing water temperatures at 20 v. 4 and 3° C for common roach *Rutilus rutilus* (L. 1758) and *O. nerka*, digestion duration increased three and eight times longer, respectively (Brett & Higgs, 1970; Hofer, 1979). Assuming these rates for *S. fontinalis*, gastric evacuation of a full stomach at 3° C would take 5 weeks. Furthermore, gastric evacuation rate is zero or lower at temperatures $\leq 2.8^\circ$ C according to the model proposed by Sweka *et al.* (2004). Evidence of little to no digestion was further supported by no significant difference in the median number of prey items consumed per season and no unidentified (*i.e.* partially digested) fish remains in winter samples.

No significant difference in the median number of prey items consumed per season also suggested continued feeding during winter, further supported by migrants actively taking ice fishing bait (A. D. Spares, pers. obs.). It appeared that low body temperatures were not negatively influencing feeding as much as digestion (Spares *et al.*, 2012). Considering that *S. fontinalis* have been shown to have lower gastric evacuation rates compared to other salmonids (Sweka *et al.*, 2004), Antigonish Harbour *S. fontinalis* may have filled their stomachs, but not emptied them during winter.

Spring median M_p and median and mean stomach fullness indices were between autumn and winter or similar to autumn indices, indicating feeding was the most consistent during this season. Although spring and autumn mean body temperatures were the same (9° C), consumption rates were comparatively higher in spring, suggesting high feeding intensity and prey availability (total n prey taxa = 32). Sea-run *S. trutta*'s consumption rates were the highest from spring to autumn (Rikardsen *et al.*, 2006). Mean stomach fullness was highest for *S. fontinalis* in St-Jean Estuary during spring (Gaudreault *et al.*, 1982), further suggesting optimum feeding conditions.

The significant increase in mean L_F , M and K from autumn to spring revealed that Antigonish Harbour *S. fontinalis* were increasing and maintaining body condition during this period. Mean K values indicated that autumn *S. fontinalis* were in very poor condition compared to migrants captured in spring, with 16% of spring specimens considered trophy class (Barnham & Baxter, 2003). Even the maximum autumn K of 1.11 was considered a poor to fair fish (Barnham & Baxter, 2003). Poor autumn K suggested that migrants had recently re-entered salt water following fasting during summer-autumn in fresh water (Morinville & Rasmussen, 2006). Only two spring

S. fontinalis (5.4%) had $K \leq 1.00$, representing poor specimens (Barnham & Baxter, 2003), which may have been individuals recently entering the harbour following overwintering in fresh water (Morinville & Rasmussen, 2006). Most spring specimens (81%) had $K \geq 1.20$, which are considered fair to excellent fish (Barnham & Baxter, 2003). Considering that many spring migrants (37%) were caught from 5 to 10 April, at least one more month of feeding was possible, subsequently increasing K even more before migrants began returning to fresh water in early May (unpubl. data).

SOURCES OF ERROR

Antigonish Harbour *S. fontinalis* are part of a special trout management area, and are heavily fished during a limited spring recreational fishery (MacMillan & Madden, 2007). Therefore, sample collection was highest during spring, with autumn and winter sampling restricted to fewer specimens to reduce negative effects on the population (Anon., 2006). It is acknowledged that low autumn and winter sample sizes represent a potentially large source of error, especially comparing seasonal feeding intensity indices and diet differences, where one or two stomachs containing high numbers of different prey could affect summary analyses. For this reason, outliers identified by Systat were removed to allow similar variances to be used for seasonal comparisons of stomach fullness, number of prey consumed and vegetal/miscellaneous mass per stomach. The cumulative taxa abundance curve showed that the maximum n of taxa consumed during autumn and winter were reached with relatively few stomachs, thus diet diversity comparisons should be unaffected by the low sample sizes.

Although fishing occurred, no samples were obtained during February, which potentially missed mid-winter trends in diet and feeding intensity. Considering samples were collected in late-January and early March, however, it is observed that migrants behaved similarly during the four-week void. Gaudreault *et al.* (1982) sampled *S. fontinalis* during February and found similar feeding patterns as spring, with prey selection focussing more on invertebrates than fishes. Other seasonal studies have had difficulty in obtaining mid-winter samples (Rikardsen *et al.*, 2006), possibly due to low movement rates of migrants (unpubl. data).

Use of 5.1 cm stretched mesh gillnets and hooks baited with live *Fundulidae* during sampling may account for larger sizes of *S. fontinalis* captured. Fyke nets were only used at the head of the tide, thus smaller fish caught in these may have inhabited the transition zone between fresh and marine waters. The resulting low sample size of smaller *S. fontinalis* (<250 mm L_F) may underestimate the importance of fishes in their diet.

Temperature, type and size of prey, predator size and prior starvation have all been shown to influence gastric evacuation rates in salmonids (Elliott, 1972). Sweka *et al.* (2004) used *S. fontinalis* approximately half the length of individuals in this study; however, they suggested that predator size would not influence gastric evacuation rates for *S. fontinalis* >152 mm L_F . Elliott (1972) found that predator size did not affect gastric evacuation rates in *S. trutta* ranging from 200 to 300 mm L_F , thus predator size effect may have been a minimal source of error in the present calculations.

Elliott (1991) showed that *S. trutta* gastric evacuation rates of Gasterosteidae were lower than of amphipods, similar to caddisfly larvae and higher than beetle larvae. Based on these data (Elliott, 1991) and Antigonish Harbour *S. fontinalis* prey (which included amphipods, caddisfly larvae and Gasterosteidae), actual evacuation rates may

have been higher than the present estimates using the Sweka *et al.* (2004) beetle and fly larvae prey model. No gastric evacuation model for piscivorous *S. fontinalis* exists, thus Sweka *et al.* (2004) was the most appropriate model for present estimates. Other consumption rate studies for fishes have used the entire digestive tract as intestine evacuation rates are lower (Héroux & Magnan, 1996). As this study used stomach contents only, estimated consumption rates may be overestimates.

ESTUARINE OVERWINTERING

Although there are benefits for anadromous salmonids overwintering in salt water, such as increased abundance of prey, stable water levels and less hazardous ice conditions (Rikardsen *et al.*, 2006), there are associated costs such as increased osmoregulation stress and possible predation (Jensen & Rikardsen, 2008, 2012). Yet, despite sea-run *S. fontinalis* experiencing Antigonish Harbour's winter extremes, such as a minimal body temperatures of -0.5°C and maximum salinity of 22.2 (unpubl. data), migrants maintained and increased body condition from November to May. Other studies have documented *S. fontinalis* overwintering in salinities ranging from 0 to 22 depending on the tide (Castonguay *et al.*, 1982; Gaudreault *et al.*, 1982; Morinville & Rasmussen, 2006). Even spring migrants within Laval Bay, Québec, tolerated a minimum temperature of 6°C in salinities reaching 34 (Curry *et al.*, 2006). Other studies (Jensen & Rikardsen, 2008, 2012) have shown *Salvelinus* sp. overwintering in full-strength sea water during winter, contradicting views that the genus is a poor osmoregulator at low temperatures (Saunders *et al.*, 1975; Finstad *et al.*, 1989; McCormick, 1994; Pennell & Barton, 1996; Claireaux & Audet, 1999). Based on diet and fishing locations, Antigonish Harbour *S. fontinalis* remained in the estuary all winter, frequently moving with the flooding tide to the head of tide mark (A. D. Spares, pers. obs.). This behaviour probably aided osmoregulation at colder temperatures (Morinville & Rasmussen, 2006).

Saltwater feeding from autumn to spring represented a valuable and important source of energy, especially for fish whose condition factor significantly decreased after freshwater fasting and spawning (Morinville & Rasmussen, 2006; Rikardsen *et al.*, 2006). Although Antigonish Harbour *S. fontinalis* diet varied with the seasons, migrants relied on a staple diet of Fundulidae and Gasterosteidae, with seasonal supplements of Gammaridae and Nereidae. Piscivory occurred in *S. fontinalis* $>250\text{ mm }L_F$; however, no predation on *Osmerus* sp. was observed, perhaps due to large prey size (A. D. Spares, pers. obs.). Stomach fullness was expected to be the lowest during winter, but the opposite was observed, which suggested that migrants continued to feed although digestion virtually ceased. It is concluded that Antigonish Harbour *S. fontinalis* undertake an autumn to spring feeding migration, during which migrants continuously maintain and increase body condition. Such a life-history strategy represents an alternative to the more common strategy of overwintering and fasting in fresh water until spring.

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