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Maternal transfer of carbon and nitrogen to progeny of sea-run and resident brook  
charr (*Salvelinus fontinalis*)

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## Abstract

Early-life history characteristics of sea-run and resident salmonid fishes that co-exist in sympatry are poorly understood. To assess differences in characteristics of offspring of these two strategies following their emergence to the stream, stable isotope ratios ( $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$ ) were used to identify the progeny of resident and sea-run female brook charr (*Salvelinus fontinalis*) in a tributary of the Miramichi River, New Brunswick, Canada. Upon emergence, sea-run progeny captured in emergence traps were longer, heavier, and had higher carbon to nitrogen ratios (C/N, an indicator of lipid content) than resident progeny, but did not have a higher body condition. After some feeding and growth in the stream, sea-run progeny (still identifiable by their  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$ ) captured in dip-nets became longer, heavier, had higher C/N, and had higher condition than resident progeny. The proportion of fish caught in dip-nets at sites where the two forms co-existed was dominated by offspring of sea-run females (sea-run = 56%, resident = 19%, unknown = 25%). These analyses suggest that offspring of sea-run, female charr benefit from maternally-derived energy reserves gained at sea and thus have potential adaptive advantages over offspring of residents.

Key words: brook trout, anadromous, stable isotopes, sympatry, life history

## **Introduction**

In coastal streams of temperate regions around the world, many populations of fishes in the family Salmonidae exist as two forms in sympatry, with resident fish completing their life cycle in the natal stream and anadromous or sea-run fish migrating to saline waters before returning to the stream to spawn (Jonsson and Jonsson 2001). Migration to more productive saline waters often yields larger body sizes in sea-run fish (Tallman et al. 1996). Due to predictable relationships between female body size and fecundity (Morita and Takashima 1998), larger anadromous females have an assumed adaptive advantage of increased fecundity over residents (Tallman et al. 1996). Sea-run fish however, are believed to have higher mortality rates associated with the challenges of migration from headwater streams to estuaries, e.g. areas with higher rates of predation by birds and mammals (Dieperink et al. 2002) and intense human fishing pressure where anglers can disproportionately target sea-run fish because of their larger body size (Roche 1992).

It is generally unknown whether potential adaptive advantages exist among different forms in the juvenile stage, particularly in the period between emergence and the end of their first year (Perry et al. 2005). Given the high rates of mortality in salmonids during the first year of life (Hutchings and Jones 1998), any competitive or survival advantages at this time could lead to selection favouring one form over the other (Hutchings 1991). Body size, lipid reserves, and condition are three relevant measures of fitness in juvenile fishes because of their importance for over-winter survival, particularly in northern latitudes (Finstad et al. 2004). Despite the importance of understanding differences between forms in early life, their identification/separation has presented a major challenge using conventional techniques (Rieman et al. 1994, Thériault and Dodson 2003).

Stable isotope analysis (SIA) has emerged as a tool to identify migratory vs. resident individuals in fish populations (Doucett et al. 1999a, McCarthy and Waldron 2000, Jardine et al. 2005a). SIA more recently has been used to trace the movement of marine organic matter into eggs and ultimately to emerging alevins in rivers (Doucett et al. 1999b) and thus the relative contribution of the two forms to juvenile production can be calculated (Charles et al. 2004, Curry 2005). Consistent differences in stable carbon ( $^{13}\text{C}/^{12}\text{C}$  or  $\delta^{13}\text{C}$ ) and nitrogen ( $^{15}\text{N}/^{14}\text{N}$  or  $\delta^{15}\text{N}$ ) isotope ratios of primary producers in marine and freshwater environments are conserved in the body tissues of fishes that reside within these two environments (France 1995). As progeny of those fishes feed and grow in natal streams, they dilute their maternal isotope ratios with new biomass, eventually adopting the isotope ratios of resident fishes (Doucett et al. 1999b). However, if sampled early enough in life, offspring of the two forms can be identified (Curry 2005).

In Beadle Brook, New Brunswick Canada, sea-run and resident brook charr (*Salvelinus fontinalis*) exist in sympatry below an impassable waterfall (Fig. 1). Earlier work conducted in 1999 using SIA found only a small contribution to overall production by sea-run charr (10%), despite a large number of adults known to be sea-run in the system (Curry 2005). This work, however, was based on a limited sample size (29 individuals below the impassable waterfall), was conducted over a short time later in the emergence period, and no measures of energy use (e.g. condition, lipid content) were taken, prompting further investigation in this system. A small contribution by sea-run fish to the overall juvenile population would have major management implications for this stock that is prized by anglers; therefore we sought to re-evaluate in more depth the contribution of the two forms over space and time in the current study.

Our objectives in this study were threefold. First, we evaluated the utility of using SIA to distinguish between sea-run and resident charr offspring (Doucett et al. 1999b, Charles et al. 2005, Curry 2005) both upon emergence and when captured in the stream soon after emergence. Second, we determined if potential adaptive advantages were apparent in energy characteristics between progeny of the two forms. Our measures of fitness were body length and weight, condition, and elemental carbon to nitrogen ratios (C/N). %C and %N data are often provided alongside stable isotope data, and high lipid tissues have higher C/N (McConnaughey and McRoy 1979) which makes C/N an index of lipid content. Our third and final objective was to assess the relative contribution of sea-run and resident females to juvenile production in the stream to compare with an earlier estimate that had indicated a low proportion of offspring of sea-run females (Curry 2005). All of these measures were conducted to determine the stability of the sea-run strategy in this system and to fill in gaps in our knowledge of the early life characteristics of sea-run and resident charr (Perry et al. 2005).

## **Materials and Methods**

### **Sample collection and preparation**

Beadle Brook (N 46.63° W 67.17°) is a tributary of the Miramichi River in New Brunswick, Canada (Fig. 1). Sites were selected in the main-stem of the brook and a tributary (north Beadle Brook) above and below a waterfall that is impassable to migratory fishes. A total of nine sites were selected to represent areas inhabited by resident fishes alone and those where sea-run and resident fishes existed in sympatry, and areas were targeted where redds were observed in previous surveys.

Emergence traps were set on redds at a variety of sites in the brook above and below the waterfall (Chernoff and Curry 2007). Traps were set to capture progeny of suspected sea-run

and resident fish, evaluated based on redd size (larger sea-run females construct larger redds than resident females, Curry and Noakes 1995). Traps were checked every 1-7 days (depending on emergence rates) and emergent fish removed. These fish were killed, total lengths measured (TL,  $\pm 1$  mm), transported on ice, oven dried, weighed to the nearest 0.0001 g (dry weight, DW) and ground to a homogenate for SIA. These fish will hereafter be referred to as “trap fish.”

To assess differences among sea-run and resident progeny post emergence, sampling was conducted using dip-nets from the stream banks at several locations in the brook (sites indicated on Fig.1) over the month following emergence (Curry et al. 1997). Fish were dipped from the stream (hereafter referred to as “net fish”), killed, total lengths measured ( $\pm 1$  mm), transported on ice, oven dried, weighed to the nearest 0.0001 g and ground to a fine homogenate for SIA. Whole fish isotope ratios approximate those of white muscle (Pinnegar and Polunin 1999), the most commonly used tissue for SIA. For both “trap fish” and “net fish”, condition factor ( $K$ ) was calculated as  $DW \cdot TL^{-3} \cdot 10^5$  (Ricker 1975).

In order to link isotope ratios in fishes from the main-stem and north branch of Beadle Brook with available food sources throughout the brook, benthic invertebrate samples were collected in D-nets at three sites in the main-stem (B, D, G) and one site in the north branch (H) (Figure 1). These samples were used to create expected equilibrium isotope ratios for trout following emergence and growth in the stream. Three taxa representing three different functional feeding groups (Merritt and Cummins 1996) were sampled from each site: Simuliidae (collector-filterers), Chironomidae (collector-gatherers), and Rhyacophilidae (predators). Samples were stored in ethanol prior to stable isotope analysis.

Dried invertebrate and fish tissues were weighed into tin cups at  $\sim 0.2$  milligrams for analysis of stable carbon and nitrogen isotopes. Samples were combusted in a Carlo Erba

NC2500 elemental analyzer and transported in a helium stream via continuous-flow to a Thermo Finnigan Delta Plus mass spectrometer (Thermo, Bremen, Germany). Isotope ratios are expressed in delta notation ( $\delta$  in permil, ‰) according to the formula:  $\delta X = (R_{\text{sample}}/R_{\text{standard}} - 1) * 1000$  where X is the heavier isotope ( $^{13}\text{C}$  or  $^{15}\text{N}$ ), R is the ratio of heavy to light isotope ( $^{13}\text{C}/^{12}\text{C}$  or  $^{15}\text{N}/^{14}\text{N}$ ) and standards are Vienna Peedee Belemnite carbonate (VPDB) and atmospheric nitrogen (AIR) for carbon and nitrogen, respectively. Samples were calibrated with IAEA standards CH6, CH7, N1 and N2. A commercially available standard (acetanilide) had  $\delta^{13}\text{C} = -33.5 \pm 0.2\text{‰}$  S.D.,  $\delta^{15}\text{N} = -3.0 \pm 0.3\text{‰}$  S.D., and C/N =  $6.88 \pm 0.21$  S.D. (n = 48). A single sample (emergent fry) was analyzed multiple times whenever samples were run and yielded  $\delta^{13}\text{C} = -28.8 \pm 0.1\text{‰}$  S.D.,  $\delta^{15}\text{N} = 11.0 \pm 0.2\text{‰}$  S.D., and C/N =  $3.64 \pm 0.10$  S.D. (n = 5), and sample replicates within analytical runs had an average standard deviation of 0.15‰ for  $\delta^{13}\text{C}$ , 0.19‰ for  $\delta^{15}\text{N}$  and 0.11 for C/N.

### **Classification modeling**

In order to classify sea-run and resident progeny captured in the stream (“net fish”) that had begun feeding and growing on available invertebrate prey, we used a simple isotope growth dilution model (Fry and Arnold 1982). This model can be used because the vast majority of isotopic change following a switch in diet by juvenile ectotherms is driven by growth (e.g. Fry and Arnold 1982, Vander Zanden et al. 1998). In the model, fish exponentially approach an equilibrium isotope ratio as they feed and grow in the stream.

For stable carbon, we used the formula:

$$\delta^{13}\text{C}_t = \delta^{13}\text{C}_e + (\delta^{13}\text{C}_i - \delta^{13}\text{C}_e) * (w_i/w_t)$$



where  $\delta^{13}\text{C}_t$  is predicted  $\delta^{13}\text{C}$  at time  $t$ ,  $\delta^{13}\text{C}_e$  is the  $\delta^{13}\text{C}$  when in equilibrium with the new diet,  $\delta^{13}\text{C}_i$  is the initial  $\delta^{13}\text{C}$ , and  $w_i$  and  $w_t$  are initial weight and weight at time  $t$ , respectively.  $\delta^{13}\text{C}_e$  was determined by measuring isotope ratios in charr YOY and a diet on which they were reared from emergence in the lab (Chernoff and Curry 2007). These measurements yielded diet-tissue  $^{13}\text{C}$  fractionation (muscle  $\delta^{13}\text{C}$  – diet  $\delta^{13}\text{C}$ ) of 2.3‰. Because invertebrates in Beadle Brook had a mean  $\delta^{13}\text{C}$  of -31.4‰, our expected  $\delta^{13}\text{C}$  for a YOY charr in equilibrium with its diet in the stream ( $\delta^{13}\text{C}_e$ ) was -29.1‰.

To capture the upper and lower bounds of the initial data in this equation ( $\delta^{13}\text{C}_i$ ), we plotted  $\delta^{13}\text{C}$  of “trap fish” vs. dry weight (Fig. 2). We then developed two equations for each morph that would include all *predicted* “trap fish” data within its upper and lower limits as the fish approached equilibrium with the new diet. We superimposed these predicted equilibration curves over our “net fish” of unknown parentage (Fig. 3). Those individuals whose  $\delta^{13}\text{C}$  fell within the defined bounds of the different morphs were classified accordingly.

Classification using  $\delta^{15}\text{N}$  was done following the same procedure as above but by substituting  $\delta^{15}\text{N}$  for  $\delta^{13}\text{C}$  in all cases.  $\delta^{15}\text{N}_e$ , also based on measurements made on charr fry reared in the lab, was 9.1‰. This was calculated from invertebrate isotope ratios in Beadle Brook ( $\delta^{15}\text{N} = 5.6\text{‰}$ ) and diet-tissue fractionation in the lab of 3.5‰. If the two isotopes yielded different classification (e.g.  $\delta^{13}\text{C}$  indicated a resident progeny and  $\delta^{15}\text{N}$  indicated a sea-run progeny), the fish was excluded from the analysis. This occurred in only 12 cases (of 196 total “net fish”), indicating good agreement between  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$ .

## Statistics

For fish captured in emergence traps (“trap fish”), unique stable isotope ratios allowed separation of three groups of progeny – sea run, main-stem resident, and tributary resident. We

used single factor analysis of variance (ANOVA) to test for differences in TL, DW, *K* and C/N in progeny of these three groups. For fish captured in dip-nets in the stream (“net fish”), due to overlapping  $\delta^{15}\text{N}$  values between the two resident populations in our model (Fig. 4), our isotope dilution model only allowed separation of two groups – sea run progeny and resident progeny. We used single factor analysis of variance (ANOVA) to test for differences in TL, DW, *K* and C/N in progeny of these two groups. Following classification of YOY captured in nets in the stream, we were able to estimate the proportion of the total catch from sea-run and resident females (residents included subpopulations in the main-stem and tributary).

## Results

A total of 127 YOY charr were captured in emergence traps (“trap fish”). These trap fish separated into three clearly distinct groups based on  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  (Fig. 4). Two groups of residents were apparent, one in the main-stem of Beadle Brook ( $\delta^{13}\text{C} = -29.0 \pm 0.4\text{‰}$  S.D.,  $\delta^{15}\text{N} = 10.6 \pm 0.8\text{‰}$  S.D.,  $n = 31$ ) and one in the north branch of the brook ( $\delta^{13}\text{C} = -32.9 \pm 0.5\text{‰}$  S.D.,  $\delta^{15}\text{N} = 9.7 \pm 0.5\text{‰}$  S.D.,  $n = 21$ ). These two groups had isotope ratios that corresponded with invertebrate prey available in the two habitats (main-stem inverts:  $\delta^{13}\text{C} = -30.6 \pm 1.6\text{‰}$  S.D.,  $\delta^{15}\text{N} = 5.4 \pm 1.5\text{‰}$  S.D.,  $n = 11$  pooled samples, north branch inverts:  $\delta^{13}\text{C} = -34.0 \pm 1.7\text{‰}$  S.D.,  $\delta^{15}\text{N} = 6.1 \pm 0.4\text{‰}$  S.D.,  $n = 3$  pooled samples). Progeny of sea-run females were highly enriched in  $^{13}\text{C}$  and  $^{15}\text{N}$  relative to the two resident groups (sea-run  $\delta^{13}\text{C} = -19.8 \pm 0.7\text{‰}$  S.D.,  $\delta^{15}\text{N} = 17.6 \pm 0.7\text{‰}$  S.D.,  $n = 63$ , Fig. 4). Isotope ratios of sea-run progeny indicated a maternal diet of invertebrates and small fishes in the Miramichi estuary, based on data obtained from Pastershank (2001) (Fig. 4).

There were differences in dry weights ( $F = 86.05$ ,  $p < 0.001$ ), total lengths ( $F = 107.88$ ,  $p < 0.001$ ) and C/N ( $F = 4.12$ ,  $p = 0.018$ ) among progeny of different morphs captured in

emergence traps, but no differences in  $K$  ( $F = 0.51$ ,  $p = 0.600$ ). Residents from the north branch of the brook were significantly shorter and lighter than residents from the main-stem, and progeny of sea-run females were longer and heavier and had higher C/N than both resident groups (Table 1).

A total of 239 YOY charr were captured using dip-nets from the stream banks (“net fish”) and 184 were successfully classified as progeny of sea-run or resident fish using our model. Following classification, we were able to test for differences in body size, condition and C/N among “net fish” progeny of sea-run and resident females. Sea-run progeny were significantly longer, heavier, had higher C/N than residents ( $F = 31.945$ ,  $p < 0.001$ ) and surprisingly also had higher  $K$  ( $F = 5.890$ ,  $p = 0.016$ ) (Table 2).

Sea-run progeny made up 5-100% of the catch at sites below the impassable waterfall, with an average contribution of 56% (Fig. 5). Below the waterfall, residents made up 0-50% of the catch, with an average of 19%. The remainder (25%) consisted of unknown individuals that we were unable to classify. Above the waterfall, no progeny were mistakenly classified as sea-run (Fig. 5), with all individuals classified as resident or unknown.

## **Discussion**

Our results indicate that progeny of sea-run females are afforded potential adaptive advantages during their early stages of development through the transfer of energy resources acquired at sea. In the Beadle Brook system, sea-run progeny dominate the population below the waterfall where the two forms exist in sympatry. These results suggest that for some environments, e.g., waters with appropriate habitat to support larger bodied, sea-run fish, the sea-run strategy is favoured during early life either as a heritable characteristic distinct from the

resident strategy (Chernoff and Curry 2007) or as a plastic response to environmental conditions that enhances fitness at the population level (Olsson et al. 2006).

Progeny of sea-run fish were larger and had higher condition than progeny of resident fish despite having a later average emergence date (Chernoff 2006). Given the lack of difference in condition between resident and sea-run progeny at emergence (“trap fish”), it was surprising that individuals captured from the stream margins (“net fish”) showed differences in condition. Potentially, the conversion of more abundant lipid reserves as indicated by higher C/N (McConnaughey & McRoy 1979) is a possible key factor leading to increased condition over time during the first summer for sea-run progeny. Sea-run progeny showed an increase in K from 0.124 to 0.138 from emergence to their capture as free-swimming alevins or fry that occurred in concert with a reduction in C/N from 4.13 to 3.87. Resident progeny also showed a reduction in C/N between samples, but did not exhibit a parallel rise in condition. In a controlled laboratory experiment, Chernoff & Curry (2007) also observed greater condition over the first summer in sea-run progeny from Beadle Brook, yet differences in body size were not apparent in another population with sea-run fish (Doucett et al. 1999b). Differences in condition and body size in the former study persisted until late August. Enhanced body size and condition in sea-run progeny could have population level consequences because larger stream fishes with more abundant body reserves are more likely to survive the first winter of life (Hutchings 1991, Finstad et al. 2004, Bystrom et al. 2006). Also, the greater energy reserves carried by progeny of sea-run females could allow easier access to faster currents in streams, which may in turn necessitate greater food consumption and increase the likelihood of a future migration to sea (Morinville and Rasmussen 2003, 2006b). If the propensity to migrate to sea is heritable, then increased survival of sea-run juveniles could lead to a higher proportion of sea-run adults in the

population, i.e., if there are habitats to support large, sea-run adults. Alternatively, migration to sea may be plastic in response to changing environmental conditions including factors such as fishing mortality (Hutchings 2005), i.e., recreational fishers of sea-run brook charr, and conditions in the stream (e.g. food availability, Olsson et al. 2006).

Based on the dramatic separation in  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  between sea-run progeny and our most  $^{13}\text{C}$ - and  $^{15}\text{N}$ -enriched resident progeny, it appears that brook charr in this population are capital breeders because they use resources for reproduction acquired far away from the breeding grounds (Bonnet et al. 1998, Houston et al. 2007). Had this sea-run population consisted of income breeders, we would have observed a continuous isotopic gradient from the resident forms up to the most elevated  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  because sea-run females feeding in freshwater would dilute the marine isotope ratios in their egg tissue. Tagging studies with Beadle Brook sea-run adults have revealed that some fish leave the stream post-spawning (November-December), arriving and wintering at the head of tide area, make some forays into the estuary for a few weeks in spring (April-May), and return to Beadle Brook by June (R.A. Curry, unpublished data; see also van de Sande 2004). Stable carbon ratios in sea-run progeny (-20‰) in the current study were similar to those for adult brook charr feeding in an estuarine fiord (Morinville and Rasmussen 2006a), but stable nitrogen ratios were enriched in  $^{15}\text{N}$  ( $\delta^{15}\text{N} = 18\text{‰}$ ) relative to sea-run charr from the same study (~12‰, Morinville and Rasmussen 2006a). This suggests considerable piscivory of marine species by Beadle Brook females, consistent with that observed for fish above 25 cm in length (Morinville and Rasmussen 2006a). When and where they forage remains somewhat unresolved. During the winter period, sea-run adults rarely move (Curry et al. 2002, Curry et al. 2006) and foraging is likely greatly reduced at low temperatures (Koskela et al. 1997). Regardless, the Miramichi River estuary where the adults are located has an

abundance of estuarine prey species, e.g., mummichog (*Fundulus heteroclitus*) and tomcod (*Microgadus tomcod*). In late winter and early spring as brook charr become active, they could be consuming anadromous rainbow smelt (*Osmerus mordax*) and alewife (*Alosa pseudoharengus*) that move from the sea into the river as the brook charr begin returning upstream. This short period may be the critical time for growth and gonad development in sea-run brook charr (Hutchings 1991, Tyler and Sumpter 1996).

An alternative explanation of the high  $\delta^{15}\text{N}$  in sea-run progeny observed in Beadle Brook may be the preferential incorporation of  $^{15}\text{N}$  over  $^{14}\text{N}$  into egg tissue due to the predominance of particular amino acids, or it may reflect the recycling of nitrogen within the developing embryos that could also lead to  $^{15}\text{N}$  enrichment (Hobson et al. 1993). Other studies have shown evidence of slight  $^{15}\text{N}$  enrichment in egg and alevin tissue relative to that of adult muscle or fin tissue ( $\sim 1\text{‰}$  in slimy sculpin, *Cottus cognatus*, Jardine et al. 2005b,  $\sim 2\text{‰}$  in coho salmon, *Oncorhynchus kisutch*, Bilby et al. 1996); while these differences are small, they could explain the difference in  $\delta^{15}\text{N}$  between sea-run progeny (mean  $\delta^{15}\text{N} = 18\text{‰}$ ) and potential fish prey from the Miramichi estuary ( $\delta^{15}\text{N} \approx 13\text{‰}$ , Pastershank 2001) after accounting for trophic fractionation.

We predict that our classification of sea-run and resident fish was conservative for “net fish”. For example, individuals that had high  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  for a given body size (Fig. 4) are likely sea-run progeny, but because they fell outside the bounds predicted for sea-run progeny coming into equilibrium with a stream diet, they remained classified as unknown. Similarly, those fish with low  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  for a given body size were also classified as unknown despite likely being offspring of resident females. Capturing fish immediately after emergence almost guarantees 100% classification using stable isotopes, as observed for “trap fish” in the current

study (providing a high degree of resolution with residents separating further into two groups) and for emerging brown trout in Brittany, France (Charles et al. 2004). For “net fish”, in comparison to earlier methods using otoliths to classify progeny of sea-run and resident salmonids (e.g., Rieman et al. 1994), our method successfully classified ~75% of all fish captured swimming in the stream which was slightly higher than that reported for otoliths (~65%, Rieman et al. 1994). Using otoliths to determine maternal origin is cumbersome analytically and requires validation of source strontium to calcium ratios that are used to identify rearing areas (Rieman et al. 1994). SIA, meanwhile, has advanced analytically to allow rapid sample preparation and throughput, is now available commercially, and has a large body of literature documenting baseline isotope ratios across a wide range of aquatic habitat types (Fry and Sherr 1984, France 1995). The technique of separating sea-run and resident fish in this study could be applied to many ecological and evolutionary questions, such as the use by sea-run juveniles of faster currents in rivers due to higher energy demands and food consumption rates (Morinville and Rasmussen 2003, 2006b). Indeed, our sample collection techniques (netting fish near the stream banks) may have underestimated the number of sea-run progeny below the waterfall if they inhabited faster currents in the centre of the stream.

The major limitation of the isotope approach remains the loss of the maternal signal during growth in the stream (Curry 2005) that creates a window of opportunity wherein progeny of resident and sea-run females can be distinguished, after which the differences are no longer apparent (Curry 2005). This window of opportunity is limited due to rapid growth rates of fish in early life, on the order of 1-2 months post emergence, corresponding to a relatively small body size (e.g. ~30 mm fork length) and may occur even faster in other species (e.g. ~2 weeks post-emergence and ~20 mm total length in smallmouth bass, Vander Zanden et al. 1998).

The high proportion of sea-run progeny making up the catch below the impassable waterfall (average = 56%) is far higher than that observed in a prior study in this system (10%, Curry 2005). The higher contribution we observed would be predicted based on the consistently large numbers of sea-run females moving in and out of the lower reaches each year. The prior estimate of 10% sea-run progeny for this system was most probably an artifact of limited sampling in space and time, or an overestimate of the resident contribution due to sampling after sea-run progeny had grown enough to come into equilibrium with their new diet of stream insects. Curry (2005) hypothesized that sea-run progeny could have dispersed downstream at the time of sampling, but with the decreasing ability to resolve sea-run from resident progeny over time, there was no strong evidence of increased proportions of resident progeny later in the emergence period in the present study. However, decreases in the proportion of sea-run progeny between sampling dates (e.g. 80% to 10% at site B from April 28<sup>th</sup> to May 17<sup>th</sup>, 90% to 5% at site D from April 27<sup>th</sup> to May 17<sup>th</sup>) were more dramatic than those observed in resident progeny, suggesting possible downstream dispersal of sea-run progeny.

The use of SIA to classify progeny as sea-run or resident continues to improve our knowledge of reproductive and early life history tactics and strategies for sympatric populations. Given the potential adaptive advantages of larger body size, higher condition, and greater lipid reserves, it is perhaps not surprising that the scope for growth is much greater in sea-run progeny (Morinville and Rasmussen 2003, Chernoff and Curry 2007). However, given that genetic differentiation between sea-run and resident salmonid forms is relatively rare (Perry et al. 2005, Charles et al. 2006) and absent in this particular population (Rogers and Curry 2004), it is unknown whether the decision to migrate is indeed heritable. The stable isotope approach therefore tells us little about the future life history strategy of progeny of the two forms, and



other techniques (e.g. back-calculated growth rates, genetic analyses) will be required to address those questions. Migration studies of progeny of sea-run and resident females reared in semi-natural enclosures hold promise in providing links between the life history strategy adopted by the parent and that of their progeny. Regardless, the sea-run strategy appears to impart adaptive advantages for progeny in the first year of life, both in terms of numbers of offspring produced (Theriault et al. 2007a) and the energy characteristics of those progeny. Whether this represents divergent selection of a heritable characteristic, a plastic response to balance the risks associated with going to sea, or most likely, a combination of both processes (Theriault et al. 2007b) there are significant implications for the survival and long-term stability of individuals and populations.

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Table 1. Total length (mm), dry weight (g), condition ( $\text{g cm}^{-3} \cdot 10^5$ ) and C/N of sea-run and resident brook charr captured in emergence traps in Beadle Brook, New Brunswick, Canada.

Residents are classified in two separate groups – main-stem and north Beadle Brook. Different letters indicate significant differences at  $\alpha = 0.05$  (ANOVA).

YOY origin	Total Length (mm)	Dry Weight (g)	K ( $\text{g cm}^{-3}$ )	C/N	n
Sea run	$23.4 \pm 0.2^a$	$0.0155 \pm 0.0003^a$	$0.124 \pm 0.004^a$	$4.13 \pm 0.04^a$	73
Resident					
(mainstem Beadle Brook)	$20.4 \pm 0.2^b$	$0.0106 \pm 0.0004^b$	$0.128 \pm 0.007^a$	$3.98 \pm 0.05^b$	32
(north Beadle Brook)	$19.0 \pm 0.3^c$	$0.0082 \pm 0.0005^c$	$0.118 \pm 0.006^a$	$3.95 \pm 0.06^b$	22



Table 2. Total length (mm), dry weight (g), condition ( $\text{g cm}^{-3} \cdot 10^5$ ) and C/N of sea-run and resident brook charr captured in dip-nets in Beadle Brook, New Brunswick, Canada. Different letters indicate significant differences at  $\alpha = 0.05$  (ANOVA).

YOY origin	Total Length (mm)	Dry Weight (g)	K ( $\text{g cm}^{-3}$ )	C/N	n
Sea run	$25.0 \pm 0.3^a$	$0.0221 \pm 0.0008^a$	$0.138 \pm 0.002^a$	$3.87 \pm 0.02^a$	101
Resident	$23.3 \pm 0.5^b$	$0.0165 \pm 0.0010^b$	$0.129 \pm 0.003^b$	$3.74 \pm 0.02^b$	83

## Figure legends

Figure 1. Location of the study area – Beadle Brook, New Brunswick, Canada. Sites A-F are below a waterfall that is impassable to migratory fishes. Sites G-I are above the waterfall.

Figure 2. Stable carbon (a) and nitrogen (b) isotope dilution curves for brook charr progeny in Beadle Brook New Brunswick, Canada as they come into isotopic equilibrium with invertebrates from the stream. Curves were generated to capture all observed data from emergence traps for progeny from the three sources (diamonds = progeny of sea-run females, squares = progeny of resident females from the main-stem, triangles = progeny of resident females from north Beadle Brook).

Figure 3. Stable carbon (a) and nitrogen (b) data vs. dry weight for brook charr progeny captured in dip-nets in Beadle Brook New Brunswick, Canada. Curves are as described in Figure 3, and all fish falling inside the bounds of one curve were classified as sea-run or resident progeny accordingly. Fish with isotope ratios outside the bounds of all curves were classified as unknown.

Figure 4. Dual isotope biplot ( $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$ ) of emerging brook charr progeny in Beadle Brook, New Brunswick, Canada. Triangles indicate progeny of resident charr (shaded) and invertebrates (open; mean  $\pm$  S.D.) from north Beadle Brook, squares are progeny of resident charr (shaded) and invertebrates (open; mean  $\pm$  S.D.) from the main-stem Beadle Brook, and diamonds are progeny of sea-run charr (open) and small fishes (solid; mean  $\pm$  S.D.) and invertebrates (open; mean  $\pm$  S.D.) from the Miramichi estuary. Data for the Miramichi estuary are modified from Pastershank 2001.

Figure 5. Estimated proportion of catch for progeny of sea-run (solid bars), resident (shaded bars) and unknown (open bars) female brook charr in Beadle Brook, New Brunswick, Canada.

Site codes are as in Figure 1. Dates are: 1 – April 27<sup>th</sup>, 2 - April 28<sup>th</sup>, 3 – April 29<sup>th</sup>, 4 – May 3<sup>rd</sup>,  
5 – May 17<sup>th</sup>.

Figure 1.

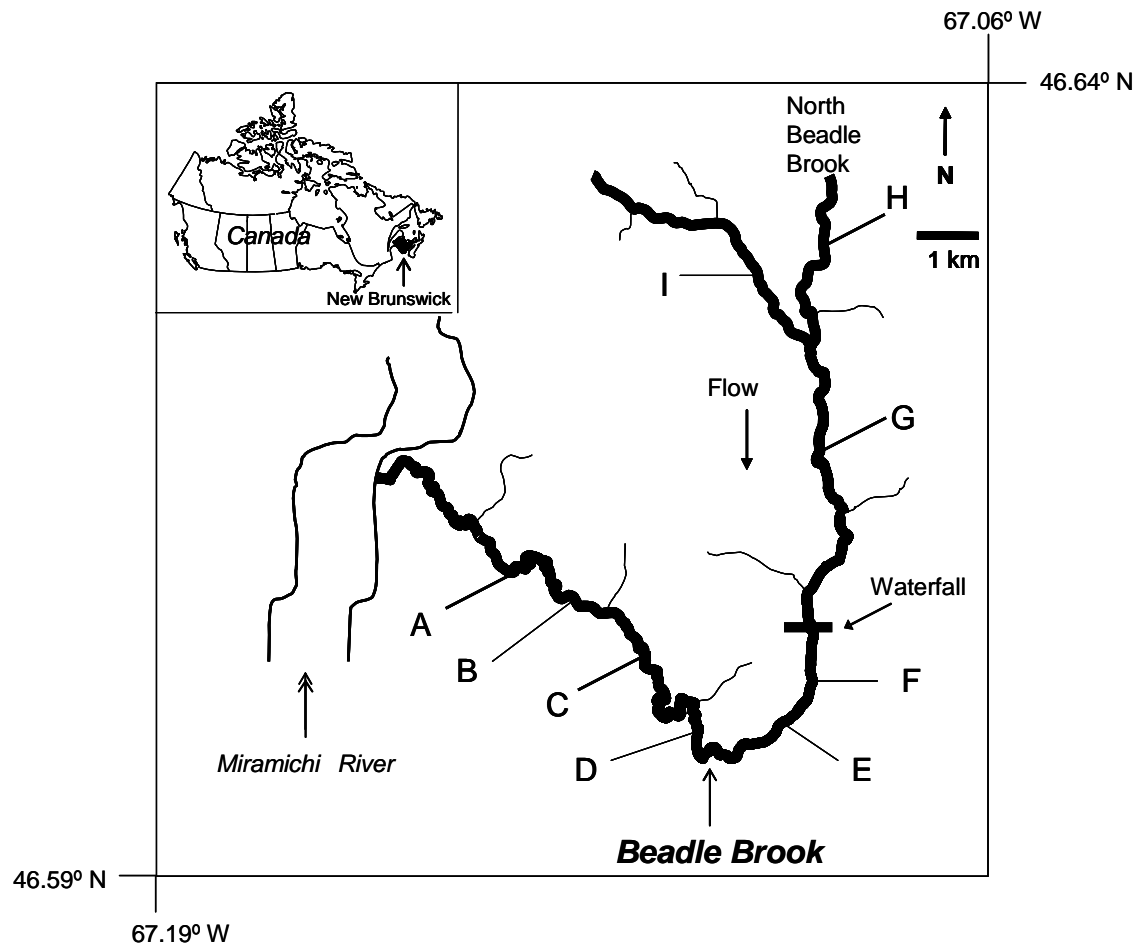


Figure 2

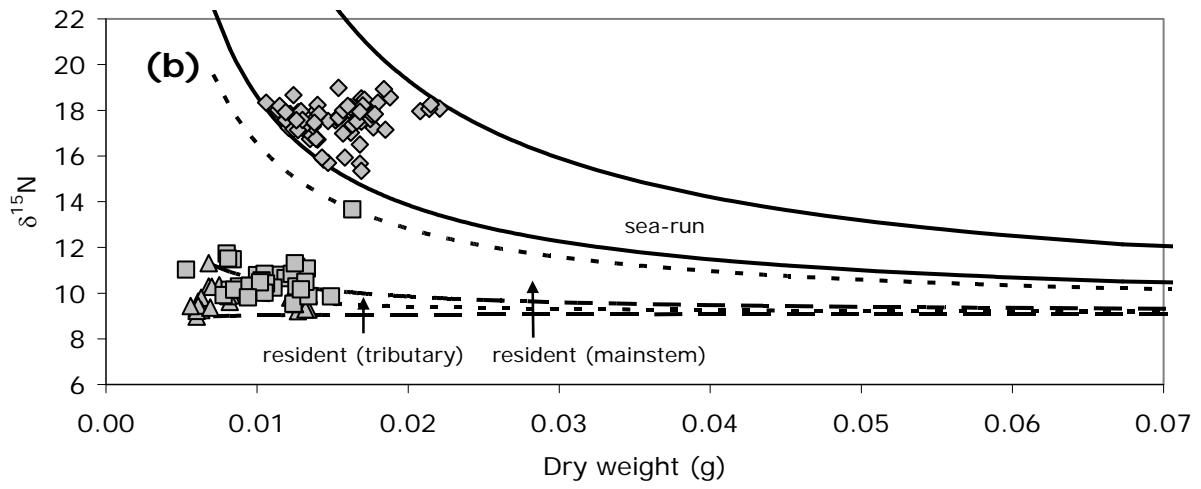
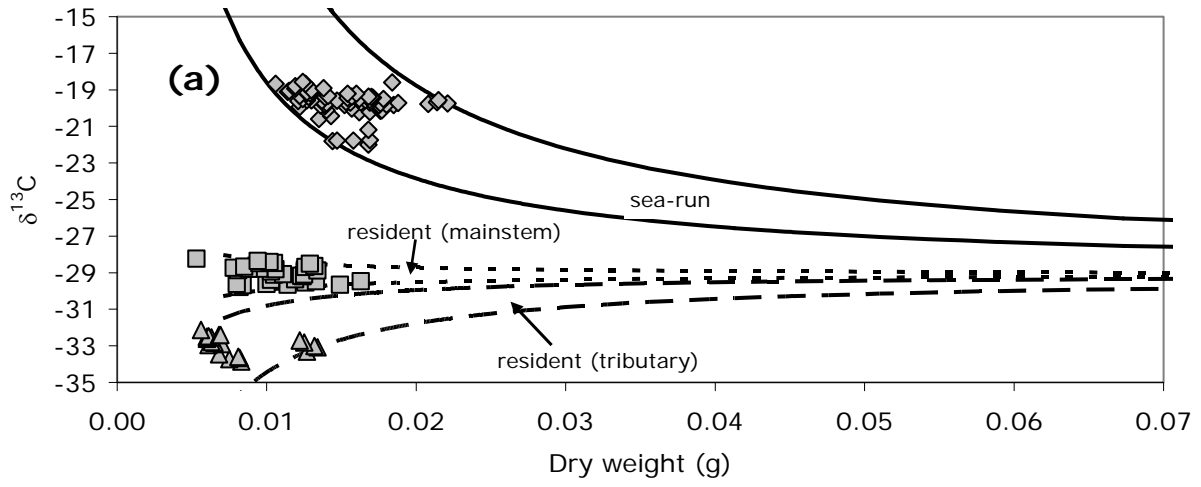


Figure 3

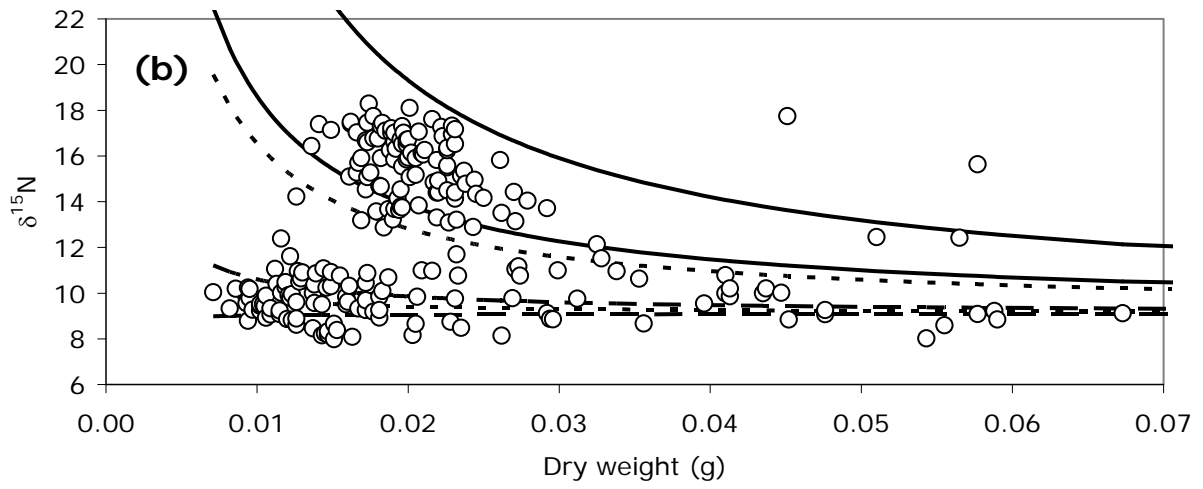
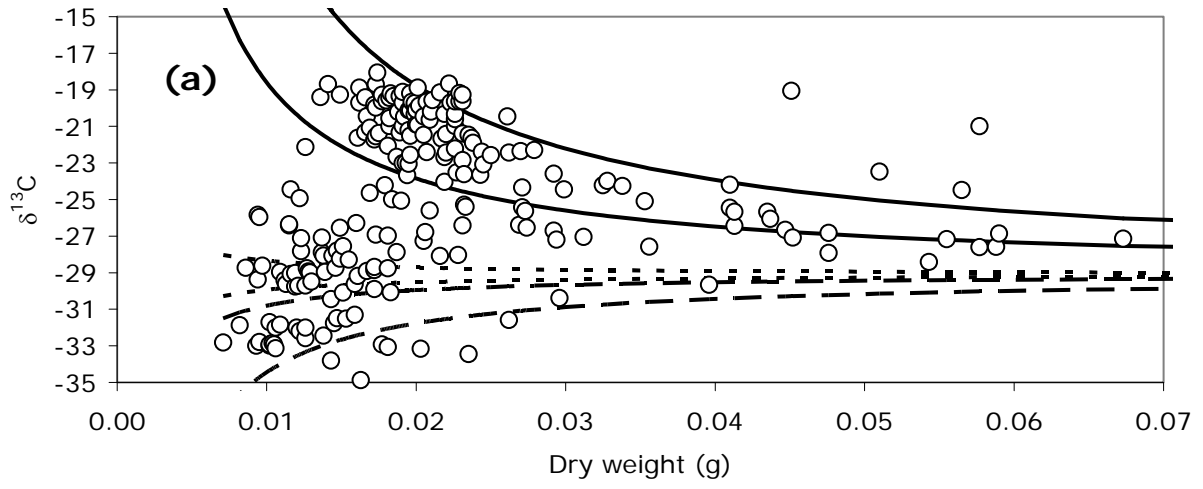


Figure 4

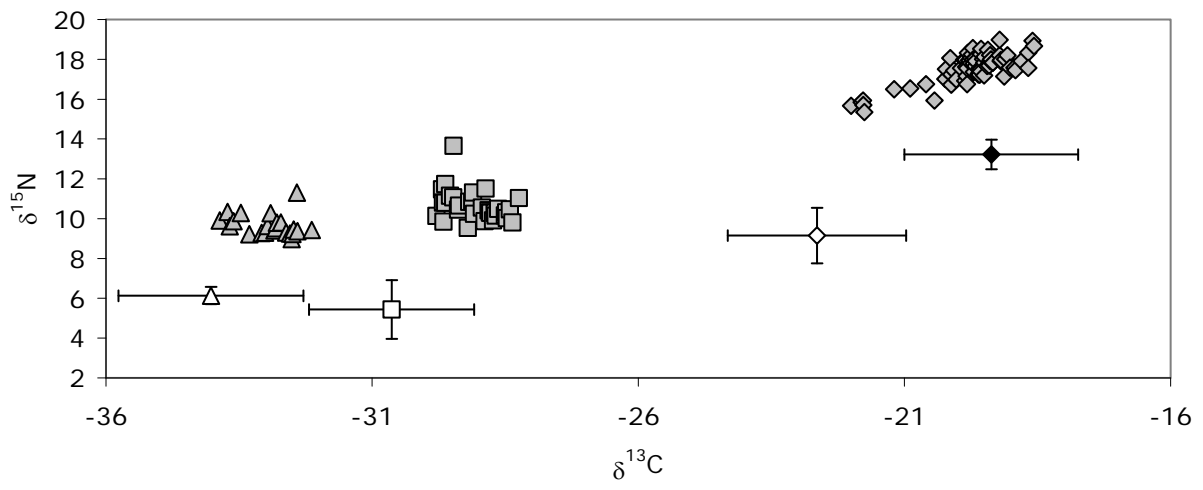
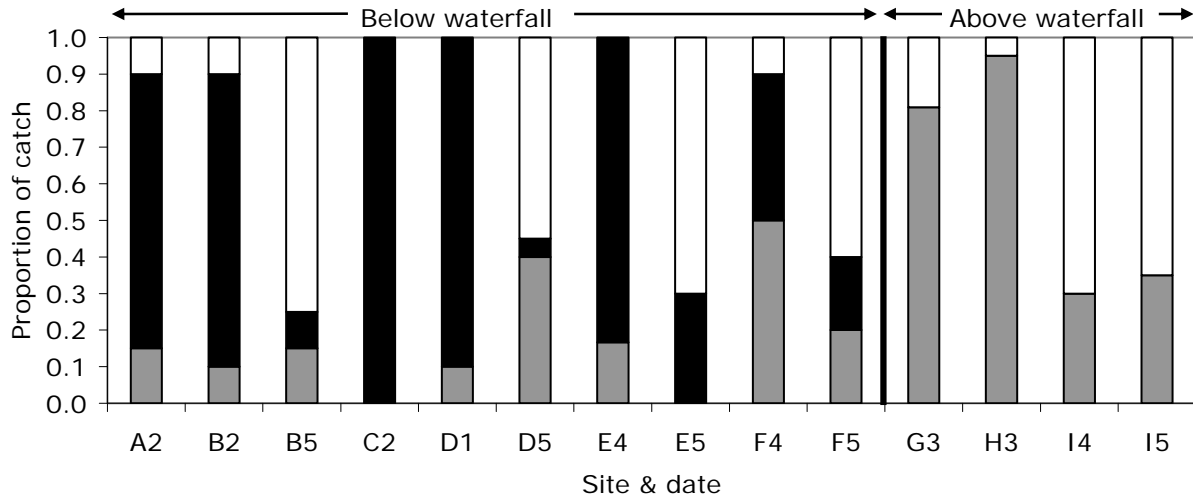


Figure 5



**Table 1.** Comparison of fits for each of four model types fit to each of four time series of baseline stable isotope data.

	Zoobenthos $\delta^{13}\text{C}$	Zoobenthos $\delta^{15}\text{N}$	Zooplankton $\delta^{13}\text{C}$	Zooplankton $\delta^{15}\text{N}$
Model 1: $Y_t = B_0 + \varepsilon_t$	86.4	31.6	94.3	73.5
Model 2: $Y_t = B_0 + B_1 \times t + \varepsilon_t$	79.6	31.2	96.1	59.3
Model 3: $Y_t = \phi \times Y_{t-1} + \varepsilon_t$	90.9	34.6	104.7	63.4
Model 4: $Y_t = B_0 + B_1 \times t + \phi \times Y_{t-1} + \varepsilon_t$	81.5	31.0	97.3	58.8

**Note:** Table values give the Akaike information criterion for each fit; lower values indicate better fits.  $Y_t$  is the mean stable isotope ratio of C or N in zoobenthos or zooplankton in year  $t$ ,  $\varepsilon_t$  is the error at time  $t$ , with  $\varepsilon \sim N(0, \sigma^2)$ ,  $B_0$  and  $B_1$  are parameters for the intercept and slope of a linear regression, and  $\phi$  is an autoregressive memory parameter describing the strength of the connection between the stable isotope ratio in year  $t$  and year  $t - 1$ .