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Growth variability of brook charr (*Salvelinus fontinalis*) in coastal maine

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Abstract – Brook charr inhabit a wide variety of habitats and exhibit considerable growth variation within and among populations. We used biannual mark–recapture electrofishing surveys and PIT tags at two streams in coastal Maine to examine spatial and temporal variability in brook charr growth. We documented considerable stream-to-stream and year-to-year variation in the growth of coastal brook charr. Based on 2892 recaptures between 2006 and 2010, we developed a suite of linear mixed models to examine variation in individual growth rates at Stanley Brook as a function of environmental variables. We distilled physical habitat data from surveys in 2010 into principle components for entry into the growth model. Growth was related primarily to an interaction between season and body length, mean water temperature, and instream location. Growth rates were highest in the summer, and smaller individuals grew more rapidly than larger conspecifics in the same stream. Individuals using habitats closer to the head of tide grew faster than those in upstream locations. Physical habitat variation was not an important control of individual growth variation within Stanley Brook. We suggest local variability in growth rates should be considered when developing management strategies for coastal populations.

Key words: brook charr; brook trout; individual growth; growth variation; PIT tags

Introduction

Brook charr inhabit a wide variety of habitats and exhibit considerable life-history variation. Populations in coastal streams exemplify this, as spatial patterns in resource availability and growth opportunities cause some individuals to adopt migratory behaviours (Gross et al. 1988; Morinville & Rasmussen 2003). Although considerable differences in growth rates are known to exist within and among landlocked populations of brook charr (McFadden 1961; Saunders & Power 1970), far less is known about the growth of coastal populations, particularly those that inhabit small tributaries that flow directly into the sea and within the southern portion of their range where anadromy occurs.

Growth variation in brook charr has profound life-history implications as a result of its effects on body size. Vulnerability to predators and anglers alike are functions of individual size, although the implications to the individual vary across time and space. Tolerance to environmental conditions varies with size and maturity (e.g., Benfey et al. 1997; McCormick & Naiman 1984, 1985). In stream salmonids, mobility and reproductive success are often correlated with and generally enhanced by size (Hutchings 1994, 1996; Morita & Takashima 1998). Furthermore, field and laboratory studies suggest a minimum body size is required for anadromy (Wilder 1952; Dutil & Power 1980; McCormick & Naiman 1984).

Numerous factors may affect fish growth. Temperature is perhaps the single most important factor in fish growth, influencing consumption, metabolism and the behaviour of brook charr (Fry 1947; De Staso & Rahel 1994). Habitat conditions play a large role in determining the growth potential for many fishes (Hayes et al. 1996). The diet of brook charr is known to vary between habitat types (Morinville & Rasmus-

sen 2006a), and the extent and complexity of available habitat influence intraspecific competition (Grant & Kramer 1990).

While habitat conditions and prey availability generally control the growth potential of a population, intrinsic factors also influence the variation observed among individuals. Growth efficiency varies among individuals and may be linked to habitat use in some instances (Morinville & Rasmussen 2003) or patterns of energy allocation (Post & Parkinson 2001). Individual behaviours, such as habitat use and prey selection, further control the growth of a fish.

To assess individual growth rates, researchers must capture a fish on multiple occasions or growth must be inferred from calcified structures. In brook charr, size histories are difficult to decipher from scales (Stolarski & Hartman 2008), and back-calculations of growth based on other bony structures are subject to bias (Campana 1990). Individual-based mark–recapture studies are now being widely implemented to avoid this problem. However, capture and handling can also impact growth rates (Hughes 1998), and relatively little is known about the cumulative effects of repeated sampling.

We sought to examine the growth of brook charr in small coastal streams. We used data derived from intensive mark–recapture electrofishing surveys and physical habitat assessments to (i) compare body growth and size structure between systems, (ii) generate a model to examine the influence of environmental conditions on individual growth rates using a robust data set from one stream and (iii) use the model to examine the effects of repeated handling on growth.

Methods

Study sites

Our study was conducted in two coastal Maine streams located approximately 65 km apart. Both streams flow directly into tidal waters and support sympatric populations of resident and anadromous brook charr.

Stanley Brook is a small oligotrophic coastal stream on the southern end of Mount Desert Island (44° 17.8′ N 68° 14.5′ W) and flows directly into the Atlantic Ocean (Figure 1). The Stanley Brook watershed contains 3.6 km of perennial surface waters, which drain 3.8 km^2 of land. Land use is predominantly coniferous forest although suburban areas (12%) exist within the watershed. Stream width (at base flow) ranges from approximately 0.5 m in the headwaters to nearly 5 m at the head of tide. The stream is dominated by shallow riffles and runs, but numerous pools >1 m deep are present in the lower reaches. The lowermost 100 m of Stanley Brook is dominated by pools, marine detritus, very little canopy cover and variable salinity (up to 32 ppt). This reach also supports an abundant population of marine isopods during portions of the year (Kazyak personal observations). Brook charr is the predominant species in this system although eels are also present in the study area.

Cove Brook (44° 41.7′ N 68° 50.9′ W) is a second-order mesotrophic tributary to the tidal reaches of the Penobscot River and drains 28 km^2 of mixed land cover via 15 km of perennial streams (Figure 1). Cove Brook starts in an extensive beaver (*Castor canadensis*) meadow complex and flows downstream through an alder thicket and mixed mesophytic forest. Within the study area, stream width at baseflow ranges from 4 to 10 m. Physical habitat varies considerably throughout the stream, ranging from dense alder thickets over clean pebbles to large, exposed, silt-laden pools. Cove Brook supports a diverse fish assemblage and is dominated by cyprinids, suckers, eels and brook charr.

Fish collection and marking

Brook charr were collected during biannual surveys (May–June and September–October) between spring 2006 and spring 2010. We used backpack electrofishing to capture fish throughout each of our study sections. Prior to handling, each fish was chemically anesthetised. The fork length (±1 mm) of each fish was measured and recorded. Newly captured individuals were surgically implanted with a 12.5-mm passive integrated transponder tag (134.2 kHz ISO tag, Digital Angel Co., TX1411SST) into the peritoneal cavity as described by Gries & Letcher (2002). The adipose fin of each newly captured individual was clipped to identify previous captures during future surveys. Recaptured individuals were identified using a hand-held PIT scanner. Following processing, each fish was allowed to recover fully from the anaesthetic and released near its capture location (<40 m at Stanley Brook and <100 m at Cove Brook). Growth rates were compared between sites and seasons using Kruskal–Wallis tests.

Modelling growth at Stanley Brook

Stanley Brook comprised approximately 95% of our total recapture data, and we focused our initial analysis on these individuals. Individual absolute growth rates were calculated from captures from consecutive sampling occasions (Eq. 1). Because mass is sensitive to variation in gut contents and reproductive condition, we based all growth calculations on fork length measurements. Absolute growth rates
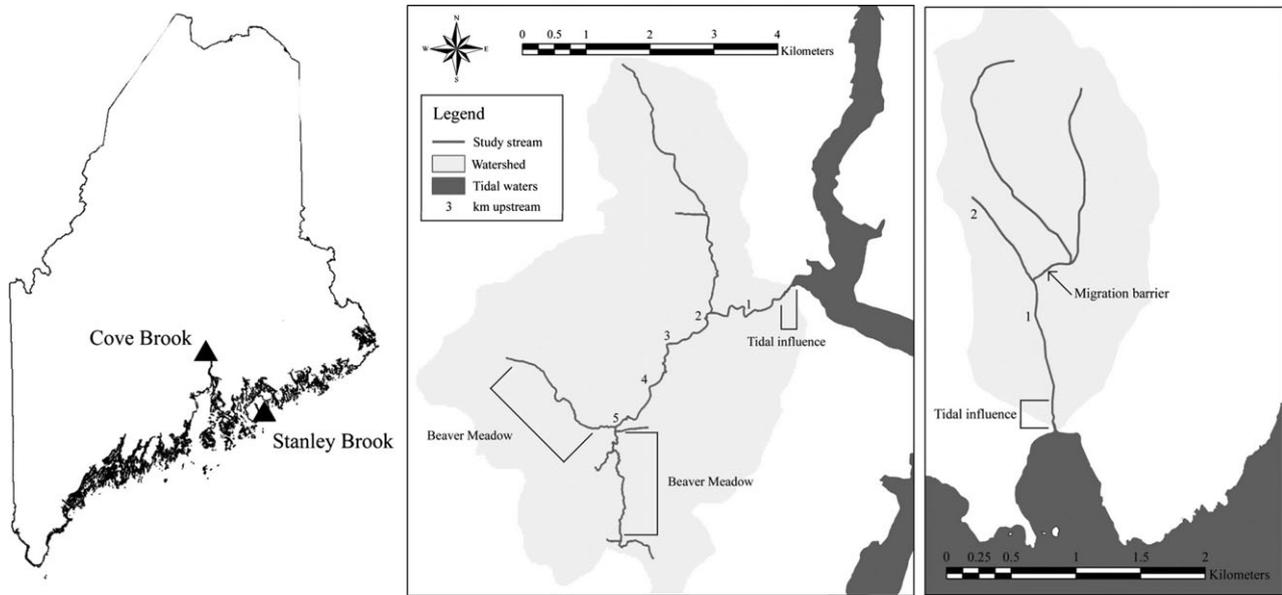
Fig. 1. We conducted intensive mark–recapture studies on two streams in coastal Maine. Cove Brook (centre) is a tributary to the tidal portion of the Penobscot River, Winterport, Maine. Stanley Brook (right) flows directly into the Atlantic Ocean on the southern shore of Mount Desert Island, Maine. Our research focused on the lower 5 km (Cove Brook) and 2 km (Stanley Brook) of each watershed.

(mm·d^{-1}) were calculated for analysis because they appear to be linear with respect to length (winter) or independent of length (summer) in our study streams (Figure 2), allowing the effect of size to be accounted for when it occurs. Other studies examining individual growth variation have also used this metric to compare growth among individuals of various sizes (Nakano et al. 1991; Xu et al. 2010).

$$\text{Absolute growth} = \frac{L_1 - L_0}{t_1 - t_0} \qquad (1)$$

We hypothesised that brook charr growth is controlled by access to marine environments or by habitat heterogeneity. We used capture data from electrofishing surveys to determine the mean along-stream location of an individual during a growth interval and used mean location (log scale) as a continuous predictor in the growth models. Habitat inventories occurred during the summer months during low-flow conditions. We used techniques based on Kazyak (1995) and Rosgen (1996) to survey channel morphology (bankfull and wetted), substrate composition and embeddedness, velocity–depth diversity, instream and dewatered woody rootwads and coarse woody debris, and canopy cover within 40-m sections. These habitat features were selected for measurement because we predicted they may be seasonally relevant to the life history of brook charr. Our habitat data were stored in 20 separate fields (see Table 1), many of which had high multicollinearity. Principle components analysis (PCA) was used to

distil habitat data into a few principle components for modelling growth.

Based on our field data, we developed a suite of *a priori* linear mixed models in Program R (R Development Core Team 2010) with the package LME4 (Bates & Maechler 2010) to describe the effects of body size, instream position, habitat, temperature, season, and year on individual growth rates (Table 2) using a similar approach to Xu et al. (2010). Season was predicted to interact with fish length, based on the relations portrayed in Figure 2. Given that many authors have reported enhanced growth rates in near-shore habitats, we predicted that individuals in the lower reaches of the streams may grow faster as a result of their proximity to tidal environments. Instream habitat conditions have been identified as a cause of growth heterogeneity, so we included the first four principle components of our habitat data in our models. Interannual and individual variation in growth rates are well documented, so these were selected as random effects and were represented in all models. Model results were used to examine the effects of repeated capture and handling on the growth of brook charr at Stanley Brook. Two binary measures of previous of capture and handling were entered into the models as fixed effects. The first measure we evaluated ('AnyHand') reflected whether the individual had been captured during any sample prior to the growth increment. The second measure ('PreHand') reflected whether or not the individual had been handled during the sampling occasion immediately prior to the growth increment. All models incorporated a normal error structure. We used
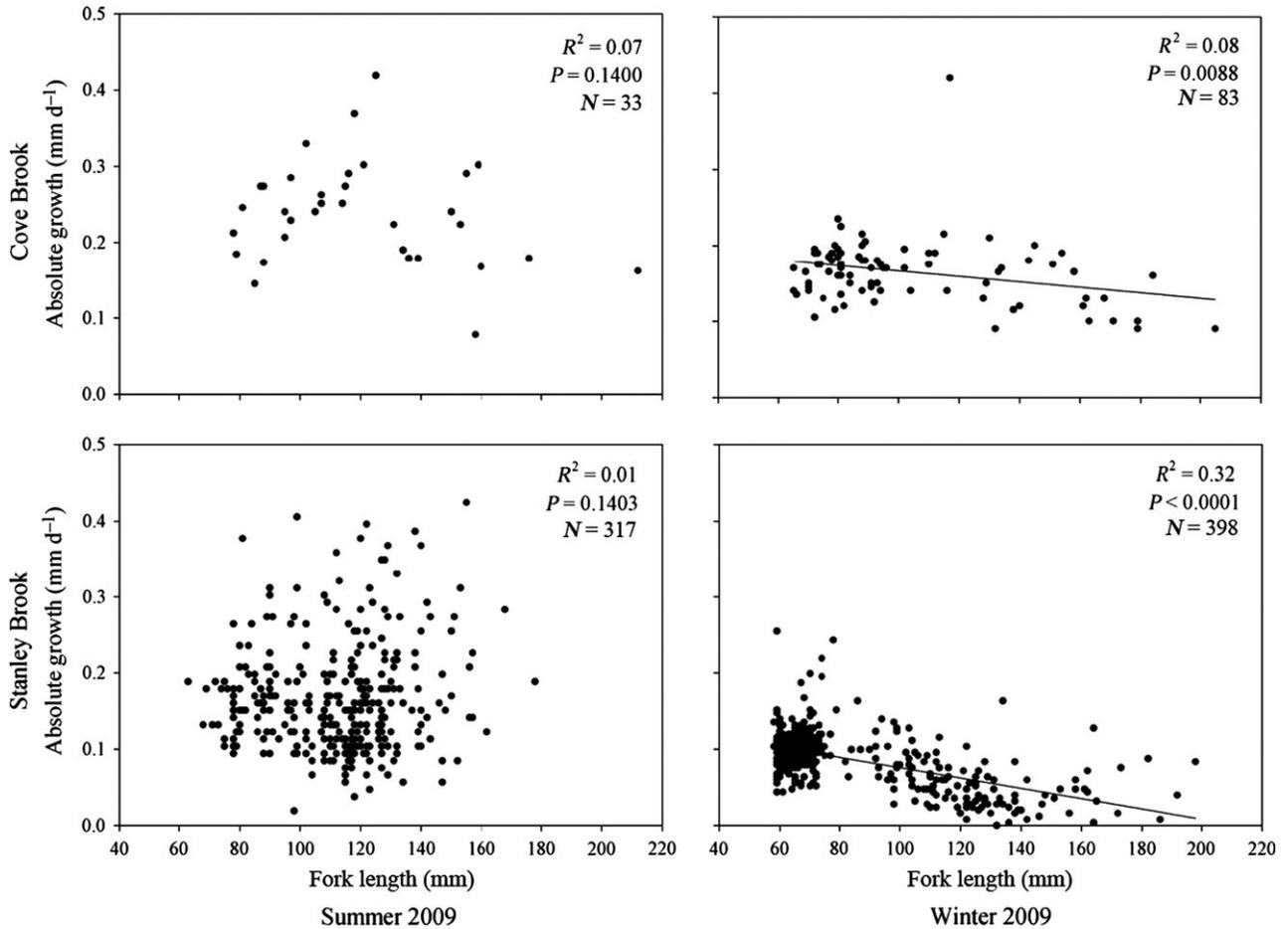
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Fig. 2. Sample relationships between fork length and absolute growth during summer and winter at Cove Brook and Stanley Brook for one year (2009). No clear patterns were observed during the summer months. In contrast, growth declined significantly ($P < 0.01$) with respect to fork length in the winter.

Table 1. Principal component loadings from habitat analysis at Stanley Brook.

	PC1	PC2	PC3	PC4
Per cent total variance explained	21.70	20.00	11.16	6.53
Velocity–depth diversity index	0.12	0.05	**0.56**	0.02
Wetted width	**0.83**	0.27	−0.10	0.10
Bankfull width	**0.83**	0.36	0.07	0.15
Bankfull cross-sectional area	**0.67**	0.52	−0.13	0.24
Wet hypsographic Index	−0.55	−0.21	−0.35	0.37
Bankfull hypsographic Index	−0.52	−0.25	−**0.44**	**0.47**
Boulder	0.59	−0.42	0.07	0.16
Cobble	0.35	−0.59	0.04	0.03
Gravel	−0.62	0.08	0.40	−0.34
Pebble	−**0.72**	0.10	0.24	0.02
Sand	−0.29	**0.65**	0.00	**0.45**
Silt/clay	0.16	0.47	−**0.66**	−0.32
Hard clay	−0.09	0.58	−0.22	−0.18
Canopy cover	0.14	−**0.66**	**0.51**	0.24
Instream coarse woody debris	−0.34	**0.77**	0.12	0.19
Dewatered coarse wood debris	−0.19	**0.68**	0.42	0.14
Instream rootwads	0.01	0.23	0.22	−0.03
Dewatered rootwads	0.14	0.24	0.34	**0.56**
Embeddedness index	0.18	0.34	0.36	−**0.47**

The four variables with the strongest loading on each principal component are represented in bold.

Akaike's information criterion (AIC) to rank competing models objectively.

Results

During the course of our electrofishing efforts, we recorded 13,674 brook charr captures at our two coastal study sites. Among these encounters, 3052 represented individuals which had been captured during the previous sampling event (2892 Stanley Brook; 160 Cove Brook), and our growth analyses were restricted to these individuals. During our surveys, individual brook charr were captured between one and eight times (Figure 3).

The brook charr in Stanley brook were considerably smaller than those in Cove Brook (Figure 4). The growth rates observed in Stanley Brook were relatively slow in the summer (0.14 mm·d^{-1} median; range 0–0.46 mm·d^{-1}) and especially in the winter (0.07 mm·d^{-1} median; range 0–0.25 mm·d^{-1}). In contrast, the growth rates we observed in Cove Brook were more rapid during both the summer (0.24 mm·d^{-1} median; range 0.08–0.66 mm·d^{-1})

Table 2. Selected models developed for comparison at Stanley Brook.

Model	Description	Structure	k	AIC_C	ΔAIC_C
A	No habitat effect	Season * FL + Temp + Temp^2 + Location + AnyHand	8	−9145.7	0.0
B	No habitat or capture effect	Season * FL + Temp + Temp^2 + Location	7	−9140.4	5.3
C	No habitat effect, capture last sample only	Season * FL + Temp + Temp^2 + Location + PreHand	8	−9137.6	8.1
D	Habitat effect	Season * FL + Temp + Temp^2 + Hab1 + Location + AnyHand	9	−9137.1	8.6
E	No habitat or interaction of season and length	Season + FL + Temp + Temp^2 + Location + AnyHand	7	−9126.7	19.0
F	No habitat or temperature effect	Season * FL + Location + AnyHand	6	−9013.7	132.0
G	No habitat or location effect	Season * FL + Temp + Temp^2 + AnyHand	7	−8889.3	256.4

Asterisks denote interactive effects. All models (A–G) also included random effects which account for individual and interannual variation (not shown). k is the number of fixed parameters for each; AIC_C is Akaike's information criterion, corrected for small sample size; ΔAIC_C is the difference between a given model and the most supported model. Model nomenclature is as follows: Season (summer vs. winter), FL (fork length; mm), Temp (temperature in Celsius), Hab1 (1st principle component of habitat), Location [Log (m upstream)], AnyHand (any previous handling), PreHand (handled immediately prior to growth increment).
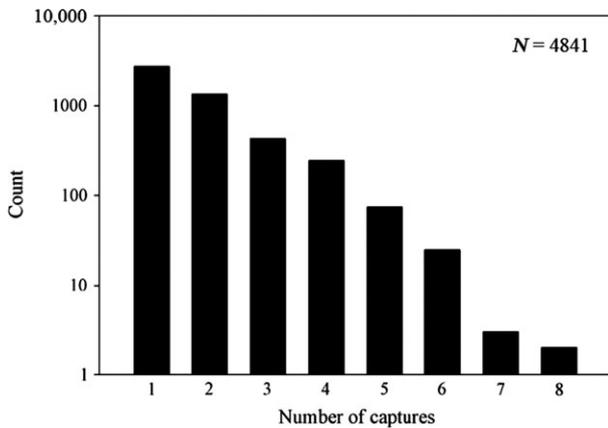

Fig. 3. Number of captures per tagged individual at Stanley Brook, 2006–2010.

and the winter (0.16 mm·d^{-1} median; range 0–0.43 mm·d^{-1}). Growth was significantly faster during the summer for both populations (Cove Brook: $\chi^2 = 44.5$, d.f. = 1, $P < 0.0001$; Stanley Brook: $\chi^2 = 43.6$, d.f. = 1, $P < 0.0001$). Additionally, growth was significantly faster for brook charr in Cove Brook during both the winter ($\chi^2 = 259.4$, d.f. = 1, $P < 0.0001$) and the summer ($\chi^2 = 835.2$, d.f. = 1, $P < 0.0001$) growth intervals.

Longevity estimates based on recapture data and growth trajectories suggest the largest individuals (>300 mm) in Cove Brook are three to four years old, whereas some of the largest individuals (200–250 mm) at Stanley Brook are in excess of six years old (and perhaps seven or eight).

Habitat data

The first four principle components accounted for 61.2% of the total variation in the raw habitat data (Table 1). The first principal component explained >21% of the variation in the data set and was dominated by measures of channel size and pebble cover (Table 1). The second principle component loaded

most heavily on coarse woody debris although sand and canopy cover were also represented strongly. The third Principle component was dominated by silt/clay and the velocity–depth diversity index. The final retained principle component was not strongly dominated by any single variable, but loaded most heavily on dewatered rootwads. These four principle components were fed into our growth model to describe the habitat conditions of each individual fish.

Growth modelling

Individual length, season, mean temperature, instream location and capture history all were found to be useful predictors of individual growth rates, as reflected in model A (Table 2). This model received the most support (weight = 0.91) and also incorporated an interaction between season and length, which suggests the relations between size and growth varies seasonally. Additionally, this model includes random year-to-year variation and variation in the inherent growth potential of individuals. Predicted growth rates were positively correlated ($R^2 = 0.66$, $P < 0.0001$) with observed growth rates in the favoured model (Figure 5).

A model (B) that included all of the variables from the favoured model (A), but did not consider a handling received substantially less support ($\Delta AIC_C = 5.3$, weight = 0.06). Interestingly, another model that considered only handling during the previous sampling event as a predictor of growth received even less support ($\Delta AIC_C = 8.1$, weight = 0.02).

Our model that included habitat as a predictor of growth was not well supported ($\Delta AIC_C = 8.6$, weight = 0.01). Other models were developed which included additional habitat data (2nd–4th principle components), but these received less support and are not reported in Table 2.

The remaining models (E–G) incorporate fewer variables than the favoured model (A) and serve to test the importance of each factor. These models
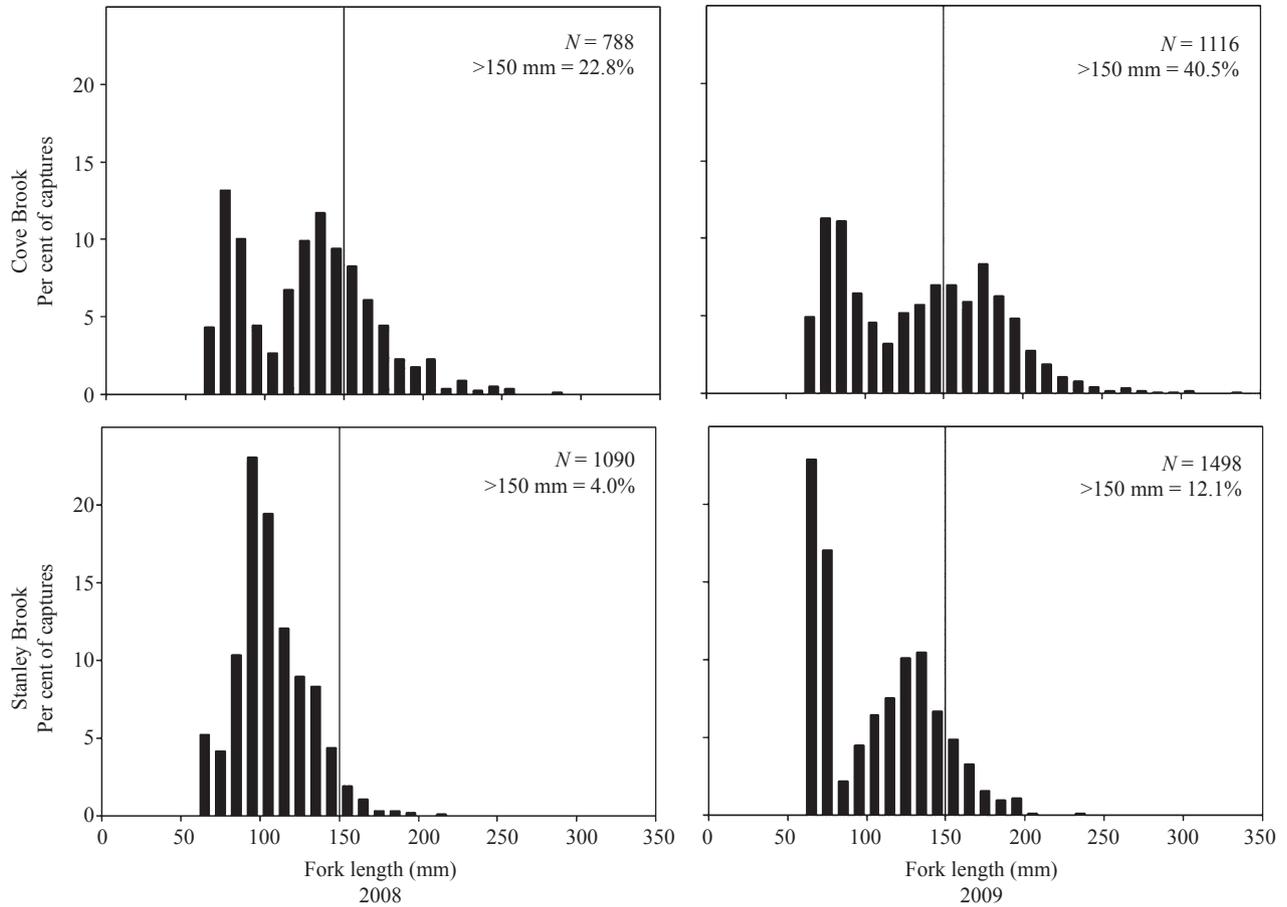
Fig. 4. Length frequency distribution of brook charr captured during fall electrofishing surveys, 2008–2009, at Stanley Brook and Cove Brook. All individuals <65 mm have been excluded from this analysis. The vertical line represents the minimum size for recreational harvest (150 mm).
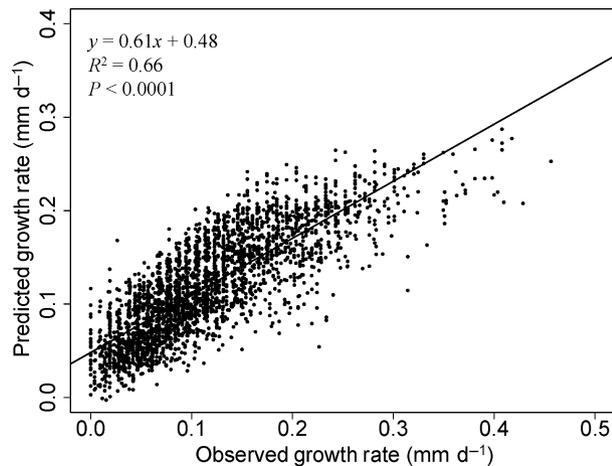

Fig. 5. The relationship between observed and predicted growth for the most supported model (a).

Table 3. Parameter estimates from the model which received the highest level of support.

Fixed Effect	Observation	Estimate ± 1 SE	
		Summer	Winter
Intercept		0.68520 ± 0.03759	0.45910 ± 0.06290
FL	mm	-0.00098 ± 0.00006	-0.00050 ± 0.00014
Temp	°C	-0.05120 ± 0.00558	
Temp^2	°C^2	0.00227 ± 0.00038	
Location	Log (m upstream)	-0.05333 ± 0.00316	
AnyHand	Capture history	-0.01096 ± 0.00260	

Random Effect		Variance ± 1 SD	
Individual		0.00043 ± 0.02083	
Year		0.00170 ± 0.04118	
Residual		0.00196 ± 0.04431	

received minimal support ($\Delta AIC_C > 7$), which suggests that the simplicity gained by omitting variables is strongly outweighed by the loss of predictive ability. Notably, lifetime capture history was determined to be an important predictor of individual growth

rates, as model C received considerably less support than model A ($\Delta AIC_C = 17.4$), which included capture history. Under the favoured model, the estimated effect of previous captures on growth was a decrease of 10.96 μm·d^{-1} (Table 3). When applied to our mark–recapture data, previous capture and handling

reduced individual growth rates by an average of 3.6% over the course of the study. This effect is smaller than the fixed effects of any of the other model variables we retained.

Discussion

We observed considerable differences in the size structure, growth and apparent longevity of two coastal brook charr populations. At Cove Brook, some brook charr grew rapidly, and three- and four-year-old brook charr sometimes exceeded 300 mm FL (Figures 2 and 4). In contrast, the brook charr population at Stanley Brook is characterised by high maximum longevity and small maximum body size (Figures 2 and 4). Based on our mark–recapture data, some individuals at Stanley Brook exceeded seven years of age while only attaining a fork length <200 mm. These differences between the streams are especially striking given the relatively short distance between the sites (<65 km).

We found substantial variation in growth rates between both Cove and Stanley Brook and within each population (range 0.0–0.66 mm·d^{-1}). While most brook charr in Cove Brook grew faster than conspecifics in Stanley Brook, some individuals in Stanley Brook achieved growth rates of >0.40 mm·d^{-1}. These fish typically used tidal habitats during the summer months and may be of special importance to future recruitment in Stanley Brook. Nonetheless, median growth rates at Cove Brook were considerably greater, and the effects are evident in the relative sizes of brook charr between the populations (Figures 4). Variation in growth and longevity is considerable between the populations and contributed to the observed differences in size structure.

In our two study systems, brook charr exhibited growth rates within the range of rates reported for other wild populations, but well below the maximum growth rates. Power (1980) reviewed existing literature and reported an average growth rate of 0.45 mm·d^{-1} during periods of rapid growth in populations from Wisconsin and Ungava. Ritzi (1959) examined the marine growth of brook charr in coastal Maine and reported an average growth rate of 0.76 mm·d^{-1} during periods at sea. The fastest growth rate he recorded was 1.45 mm·d^{-1} during a 28-day foray at sea. The observed discrepancy between our observations and the maximum rates in the literature probably reflects the longer time interval between our samples, from which our observations represent averaged growth rates. Brook charr, like many other fishes, seem to maintain a capacity for high food processing and growth despite extended periods with modest feeding opportunities (Armstrong & Schindler 2011).

Variation in growth rates

Our best model described variation in growth based on the influences of body length, season, temperature, instream position and lifetime capture history with additional random effects from interannual and individual variation and was able to effectively capture much of the observed variation in individual growth rates (Figure 5). Considering the plasticity of behaviours observed in brook charr, long intervals between recapture events, and variability in feeding and reproductive behaviours, our best model was quite effective at explaining variation in individual growth rates.

Effects of body size and season

Based on our model, the influence of body size was negative but varied by season. Median observed growth rates were substantially faster (0.07 mm·d^{-1}) in the summer, but the effect of body size was more pronounced (-0.983 μm·d^{-1}·mm^{-1} intial length) compared with the winter (-0.508 μm·d^{-1}·mm^{-1}). A general decline in absolute growth rate with increased size is not a surprising result, given that many other populations exhibit this pattern (Power 1980), and mass-specific consumption is known to decline with body size (Elliot 1976; Hartman & Sweka 2001).

Seasonal variation in growth rates is likely related to temperature, food availability and varying patterns of energy allocation. In summer months, brook charr grew rapidly in Stanley Brook. During this period, temperatures were often near optimal for growth, and food resources were more abundant. As most egg development occurs after mid-summer (Henderson 1963), surplus energy consumed during early summer can be directed primarily towards somatic growth. Accordingly, late spring and early summer have been reported as a very important period for the growth of brook charr (Utz & Hartman 2006; Xu et al. 2010). Summer feeding has been reported to replenish lipid reserves that have declined over the winter (Cunjak & Power 1986), especially in anadromous individuals feeding in the estuary. Thus, summer appears to be an important growth period for coastal brook charr populations.

In contrast to summer, our winter interval included the spawning season and extensive periods of cold weather. Reproductive activities reduce growth rates. While spawning, mature females may lose a substantial portion of their body mass and lipid reserves (Hutchings 1994). Mature males also expend a considerable portion of their energy reserves defending redd sites, so the effects are not limited to females (Hutchings 1994). During the frigid winter months, condition and energy reserves decline, even though

brook charr may continue feeding (Cunjak & Power 1986; Cunjak et al. 1987). Metabolic costs probably exceed consumption gains during this period. The negative relationship between body size and growth during our winter interval (Figure 2) relates to reduced feeding opportunities coupled with the energy expenditures associated with spawning, the costs of which can vary with size (Hutchings 1994). Larger brook charr are expected to invest proportionately more energy into reproduction and have been reported to experience greater declines in somatic lipid reserves than smaller conspecifics during a period corresponding to our winter interval (Hutchings et al. 1999).

Spatial heterogeneity in growth

Individual growth rates showed strong spatial patterns at Stanley Brook. Growth rates rapidly declined as distance from the head of tide increased (Figure 6, Table 3). Growth variability within a stream is known to be linked to life history, as anadromous individuals often exhibit enhanced growth (Dutil &

Power 1980; Morinville & Rasmussen 2006b; Chernoff & Curry 2007). Enhanced growth in the lower reaches of Stanley Brook may either represent *in-situ* feeding conditions but may also reflect feeding forays into tidal environments. Rapid growth in tidally influenced environments has been widely reported (Smith & Saunders 1958; Dutil & Power 1980; Morinville & Rasmussen 2006b). Prey such as amphipods may be an important food resource and can be very abundant near the head of tide on coastal brook charr streams (Donald et al. 1980; Morinville & Rasmussen 2006b). Extensive use of estuarine waters near the head of tide for anadromous individuals (Castonguay et al. 1982; Curry et al. 2006) suggests an important role in growth. Additionally, brook charr using tidal waters may have an inherent growth advantage, as they may grow faster in freshwater environments than stream resident conspecifics as a result of maternal and genetic advantages when food is not limiting (Chernoff & Curry 2007). Even in systems without access to tidal environments enhanced growth rates occur in downstream locations (Cooper et al. 1962; Thorne 2004).
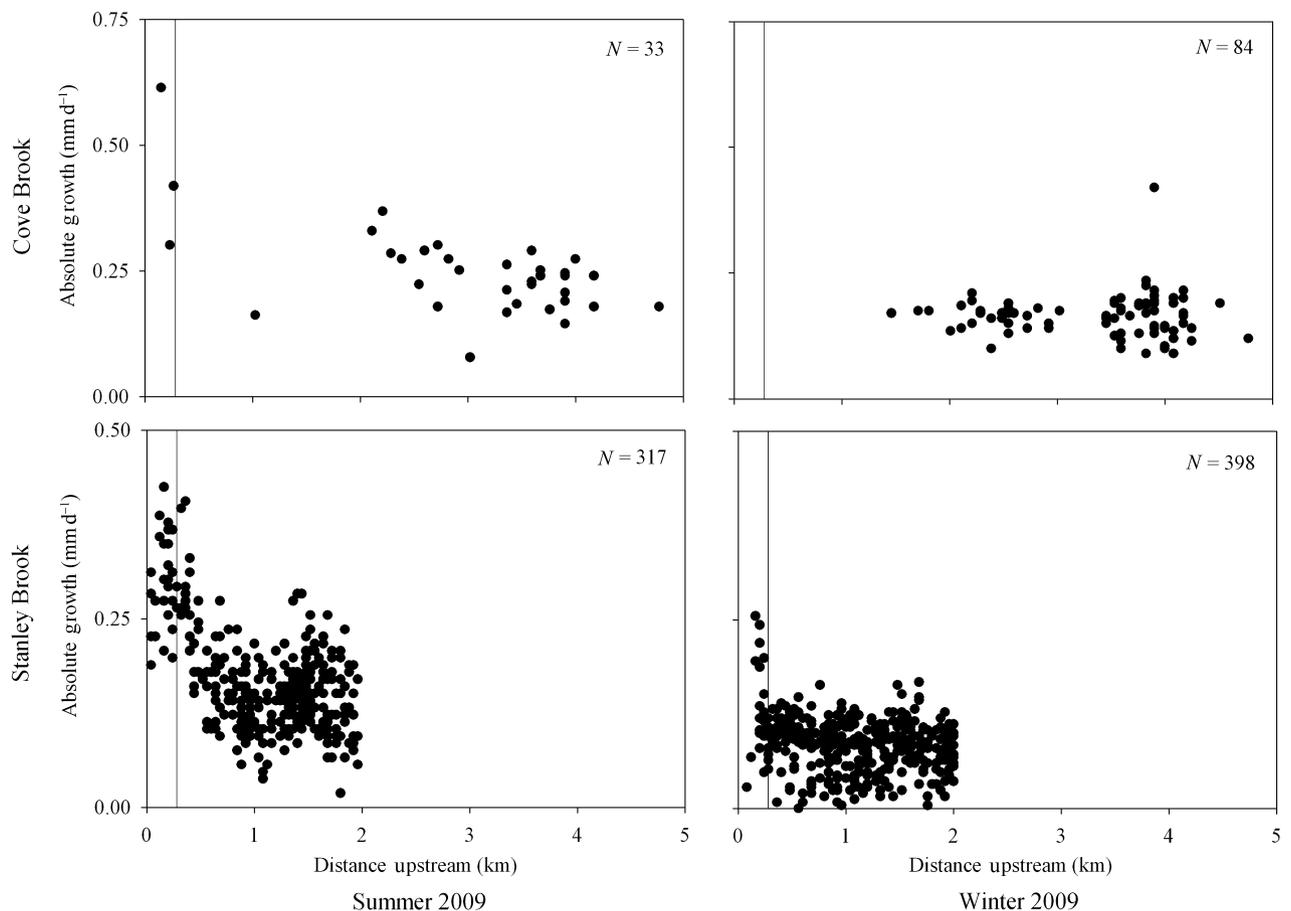

Fig. 6. Sample relationships between absolute growth and distance upstream from the mouth of Cove Brook or Stanley Brook for one year (2009). All locations based on captures at the start of a growth interval. The vertical lines delineate the portion of each stream identified as being tidally influenced.

Habitat measures were not useful in predicting brook charr growth rate in Stanley Brook. Stanley Brook is relatively homogenous upstream of the tidally influenced zone, and the location component of our model may have captured much of the variation in habitat. Additionally, individual movements could integrate the growth potential of various habitats over time, resulting in weak growth signals with respect to habitat. We assigned fish to habitat based on their location at the beginning of an sampling interval, but we were not able to follow the fish throughout the study period in real time. Movement appears to be a rare phenomenon in the Stanley Brook population (Kazyak 2011) but may still be ecologically important. Habitat is sometimes reported to influence the growth of salmonids (Bystrom et al. 2004) although this is not always the case (Gowan & Fausch 1996). Our study failed to reveal any important growth trends with respect to habitat. Spatial heterogeneity in productivity appears to drive some of the growth variation, but this effect appears to be primarily a result of tidal influence.

Interannual variation

During the course of our study, growth rates varied yearly (Table 3). Under our model, interannual growth variation is accounted for by a random effect with a variance of 1.70 $\mu m \cdot d^{-1}$ (Table 3). This effect is quite minor relative to the effects of season, length, temperature and instream position on absolute growth.

Other authors have examined interannual variation in brook charr populations and ascribed fluctuations in growth rates to water temperatures (Robinson et al. 2010). Our favoured model specifically accounts for mean water temperature (nonlinear effect; entered as a quadratic), suggesting it accounts for at least some of the observed variation between years. Given the long time intervals between recapture events that include periods of unusually hot and cold conditions, it is remarkable that mean water temperature is a useful predictor of growth rates.

Individual growth potential

We found inherent differences among individuals resulted in slight variation in growth rates (Table 3). This variation may be related to variation in metabolic efficiency, behaviour, genetics and reproductive energy expenditures (Nakano et al. 1991; Hutchings et al. 1999). Our data preclude us from a mechanistic examination of other factors which contribute to variation in individual growth, but intrinsic factors do not seem to be an important driver of growth variation within a population.

Captures

Our index of capture and handling intensity was a useful predictor of individual growth rates, but interpretation of the capture effect is not straightforward. Given the nature of the sampling programme, a collected individual may have been shocked once or twice during each sampling occasion. Additionally, individuals that were not captured may still have been subjected to stress due to electrofishing. The effect we detected may be an artefact of the study design; individuals who have been captured many times are generally older and thus larger, making the effects of repeated sampling on growth harder to detect. We attempted to minimise this risk using 'AnyHand' and 'PreHand' as predictive variables rather than the number of times an individual had been captured, which is more closely correlated with individual age. Regardless, our index of capture and handling intensity was a useful predictor of individual growth rates.

Other studies have yielded mixed conclusions on the impacts of intensive sampling on growth rates. Sigourney et al. (2005) investigated the impacts of electrofishing and PIT tagging on young, captive Atlantic salmon (*Salmo salar*) but did not detect any significant impacts on growth. Conversely, Gatz et al. (1986) found significant decreases in growth rates of wild trout with repeated electrofishing, with the strongest effects on small individuals with short intervals between samples. We intensively sampled small, wild brook charr at long intervals and found repeated handling had a small but detectable influence on individual growth rates.

Based on our field data and modelling efforts, we conclude that the effects of handling on growth are *minimal* relative to environmental effects at our study locations. This topic warrants further investigation as the effects of electrofishing and handling may vary with electrical waveform, species and size (Miranda & Kidwell 2010) and may also differ between wild and captive fish. Given the unique insights into life history afforded by intensive mark–recapture studies, the small observed impact of sampling on growth may be acceptable to many fisheries researchers.

Management implications

We found considerable variation in the growth rate of brook charr between and within populations. Despite the potential for significant spatial variability in life-history characteristics, populations are typically managed at the regional scale. Extreme life-history variability in brook charr means that regulations appropriate for one population may not be appropriate for another population (Adams & Hutchings

2003). We suggest local variability in growth rates of brook charr should be considered when developing management strategies for coastal populations. In particular, coastal populations with access to marine environments warrant special attention by fisheries managers, as growth rates appear to increase considerably with proximity to the sea.

Acknowledgements

References

Adams, B.K. & Hutchings, J.A. 2003. Microgeographic population structure of brook charr: a comparison of microsatellite and mark-recapture data. Journal of Fish Biology 62: 517–533.

Armstrong, J.B. & Schindler, D.E. 2011. Excess digestive capacity in predators reflects a life of feast and famine. Nature 476: 84–87.

Bates, D. & Maechler, M. 2010. lme4:linear mixed-effects models using s4 classes. R package version 0.999375-35. http://CRAN.R-project.org/package=lme4

Benfey, T.J., McCabe, L.E. & Pepin, P. 1997. Critical thermal maxima of diploid and triploid brook charr, *Salvelinus fontinalis*. Environmental Biology of Fishes 49: 259–264.

Bystrom, P., Andersson, J., Persson, L. & De Roos, A.M. 2004. Size-dependent resource limitation and foraging-predation risk trade-offs: growth and habitat use in young arctic char. Oikos 104: 109–121.

Campana, S.E. 1990. How reliable are growth back-calculations based on otoliths? Canadian Journal of Fisheries and Aquatic Sciences 47: 2219–2227.

Castonguay, M., FitzGerald, G.J. & Cote, Y. 1982. Life history and movements of anadromous brook charr, *Salvelinus fontinalis*, in the St-Jean River, Gaspè, Quebec. Candian Journal of Zoology 60: 3084–3091.

Chernoff, E. & Curry, R.A. 2007. First summer growth predetermined in anadromous and resident brook charr. Journal of Fish Biology 70: 334–346.

Cooper, E.L., Boccardy, J.A. & Andersen, J.K. 1962. Growth rate of brook trout at different population densities in a small infertile stream. The Progressive Fish Culturist 24: 74–80.

Cunjak, R.A. & Power, G. 1986. Seasonal changes in the physiology of brook trout, *Salvelinus fontinalis*, in a sub-Arctic river system. Journal of Fish Biology 29: 279–288.

Cunjak, R.A., Curry, R.A. & Power, G. 1987. Seasonal energy budget of brook trout in streams: implications of a possible deficit in early winter. Transactions of the American Fisheries Society 116: 817–828.

Curry, R.A., van de Sonde, J. & Whoriskey, F.G. 2006. Temporal and spatial habitats of anadromous brook charr in the Laval River and its estuary. Environmental Biology of Fishes 76: 361–370.

De Staso, J.D. III & Rahel, F.J. 1994. Influence of water temperature on interactions between juvenile Colorado River cutthroat trout and brook trout in a laboratory stream. Transactions of the American Fisheries Society 123: 289–297.

Donald, D.B., Anderson, R.S. & Mayhood, D.W. 1980. Correlations between brook trout growth and environmental variables for mountain lakes in Alberta. Transactions of the American Fisheries Society 109: 603–610.

Dutil, J.D. & Power, G. 1980. Coastal populations of brook trout, *Salvelinus fontinalis*, in Lac Guillaume-Delisle (Richmond Gulf) Quebec. Canadian Journal of Zoology 58: 1828–1835.

Elliot, J.M. 1976. The energetics of feeding, metabolism and growth of brown trout (*Salmo trutta* L.) in relation to body weight, water temperature, and ration size. Journal of Animal Ecology 45: 923–948.

Fry FEJ. 1947. Effects of the environment on animal activity. University of Toronto, Biological Series No. 55. Publication of the Ontario Fisheries Research Laboratory No. 68.

Gatz, J.A. Jr, Loar, J.M. & Cada, G.F. 1986. Effects of repeated electrofishing on instantaneous growth of trout. North American Journal of Fisheries Management 6: 176–182.

Gowan, C. & Fausch, K.D. 1996. Long-term demographic responses of trout populations to habitat manipulation in six Colorado streams. Ecological Applications 6: 931–946.

Grant, J.W. & Kramer, D.L. 1990. Territory size as a predictor of the upper limit to population density of juvenile salmonids instreams. Canadian Journal of Fisheries and Aquatic Sciences 47: 1724–1737.

Gries, G. & Letcher, B.H. 2002. Tag retention and survival of age-0 Atlantic salmon following surgical implantation with passive integrated transponder tags. North American Journal of Fisheries Management 22: 219–222.

Gross, M.R., Coleman, R.M. & McDowall, R.M. 1988. Aquatic productivity and the evolution of diadromous fish migration. Science 239: 1291–1293.

Hartman, K.J. & Sweka, J.A. 2001. Development of a bioenergetics model for Appalachian brook trout. Proceedings of the Annual Conference of the Southeastern Association of Fish and Wildlife Agencies 55: 38–51.

Hayes, D.B., Ferreri, C.P. & Taylor, W.W. 1996. Linking fish habitat to their population dynamics. Canadian Journal of Fisheries and Aquatic Sciences 53(Suppl. 1): 383–390.

Henderson, N.E. 1963. Influence of light and temperature on the reproductive cycle of the Eastern Brook Trout, *Salvelinus fontinalis* (Mitchell). Journal of the Fisheries Research Board of Canada 20: 859–897.

Hughes, N.F. 1998. Reduction in growth due to electrofishing and tagging may change interannual movement behavior of stream salmonids: evidence from Arctic grayling in an interior Alaskan stream. Transactions of the American Fisheries Society 127: 1072–1077.

Hutchings, J.A. 1994. Age- and size-specific costs of reproduction within populations of brook trout, *Salvelinus fontinalis*. Oikos 70: 12–20.

Hutchings, J.A. 1996. Adaptive phenotypic plasticity in brook trout, *Salvelinus fontinalis*, life histories. Ecoscience 3: 25–32.

Hutchings, J.A., Pickle, A., McGregor-Shaw, C.R. & Poirier, L. 1999. Influence of sex, body size, and reproduction on overwinter lipid depletion in brook trout. Journal of Fish Biology 55: 1020–1028.

Kazyak, P.F. 1995. Maryland Biological Stream Survey Sampling Manual. Maryland: Department of Natural Resources, Chesapeake Bay Research and Monitoring Division.

Kazyak, D.C. 2011. Growth and Movement of Brook Charr (Salvelinus fontinalis) in Coastal Maine. Master's thesis Orono, ME: University of Maine.

McCormick, S.D. & Naiman, R.J. 1984. Osmoregulation in the brook trout, *Salvelinus fontinalis*. II. Effects of size, age, and photoperiod on seawater survival and ionic regulation. Comparative Biochemistry and Physiology 79A: 17–28.

McCormick, S.D. & Naiman, R.J. 1985. Hypoosmoregulation in an anadromous teleosts: influence of sex and maturation. Journal of Experimental Zoology 234: 193–198.

McFadden, J.T. 1961. A population study of the brook trout, *Salvelinus fontinalis*. Wildlife Monographs 7: 3–73.

Miranda, L.E. & Kidwell, R.H. 2010. Unintended effects of electrofishing on nongame fishes. Transactions of the American Fisheries Society 139: 1315–1321.

Morinville, G.R. & Rasmussen, J.B. 2003. Early bioenergetic differences between anadromous and resident brook trout (*Salvelinus fontinalis*). Canadian Journal of Fisheries and Aquatic Sciences 60: 401–410.

Morinville, G.R. & Rasmussen, J.B. 2006a. Does life-history variability in salmonids affect habitat use by juveniles? A comparison among streams open and closed to anadromy. Journal of Animal Ecology 75: 693–704.

Morinville, G.R. & Rasmussen, J.B. 2006b. Marine feeding patterns of anadromous brook trout (*Salvelinus fontinalis*) inhabiting an estuarine river fjord. Canadian Journal of Fisheries and Aquatic Sciences 63: 2011–2027.

Morita, K. & Takashima, Y. 1998. Effect of female size on fecundity and egg size in white-spotted charr: comparison between sea-run and resident forms. Journal of Fish Biology 53: 1140–1142.

Nakano, S., Kachi, T. & Nagoshi, M. 1991. Individual growth variation of red-spotted masu salmon, *Onchyrhynchus masou rhodorus*, in a mountain stream. Japanese Journal of Ichthyology 38: 263–270.

Post, J.R. & Parkinson, E.A. 2001. Energy allocation strategy in young fish: allometry and survival. Ecology 82: 1040–1051.

Power, G. 1980. The brook charr, *Salvelinus fontinalis*. In: Balon, E.K., ed. Charrs, Salmonid Fishes of the Genus *Salvelinus*. Netherlands: W. Junk, The Hague, pp 141–203.

R Development Core Team. 2010. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0, URL http://www.R-project.org.

Ritzi, C.F. 1959. Eastern Brook Trout Populations of Two Maine Coastal Streams Master's Thesis. Orono, ME: University of Maine.

Robinson, J.M., Josephson, D.C., Weidel, B.C. & Kraft, C.E. 2010. Influence of variable summer water temperatures on brook trout growth, consumption, reproduction, and mortality in an unstratified Adirondack lake. Transactions of the American Fisheries Society 139: 685–699.

Rosgen, D. 1996. Applied River Morphology. 2nd edn. Pagosa Springs (CO): Wildland Hydrology.

Saunders, L.H. & Power, G. 1970. Population ecology of the brook trout, *Salvelinus fontinalis*, in Matamek Lake, Quebec. Journal of the Fisheries Research Board of Canada 27: 413–424.

Sigourney, D.B., Horton, G.E., Dubreuil, T.L., Varaday, A.M. & Letcher, B.H. 2005. Electroshocking and PIT tagging of juvenile Atlantic salmon: are there interactive effects on growth and survival? North American Journal of Fisheries Management 25: 1016–1021.

Smith, M.W. & Saunders, J.W. 1958. Movements of brook trout, *Salvelinus fontinalis* (Mitchill), between and within fresh and salt water. Journal of the Fisheries Research Board of Canada 15: 1403–1449.

Stolarski, J.T. & Hartman, K.J. 2008. An evaluation of the precision of fin ray, otolith, and scale age determinations for brook trout. North American Journal of Fisheries Management 28: 1790–1795.

Thorne, D.W. 2004. Spatial and Seasonal Variation in Brook Trout Diet, Growth, and Consumption in a Complex Appalachian Watershed. Dissertation. Morgantown, WV: West Virginia University.

Utz, R.M. & Hartman, K.J. 2006. Temporal and spatial variation in the energy intake of a brook trout (*Salvelinus fontinalis*) population in an Appalachian watershed. Canadian Journal of Fisheries and Aquatic Sciences 63: 2675–2686.

Wilder, D.G. 1952. A comparative study of anadromous and freshwater populations of brook trout (*Salvelinus fontinalis*). Journal of the Fisheries Research Board of Canada 9: 169–202.

Xu, C., Letcher, B.H. & Nislow, K.H. 2010. Context-specific influence of water temperature on brook trout growth rates in the field. Freshwater Biology 55: 2253–2264.