

## A Roadmap for Coasters: Landscapes, Life Histories, and the Conservation of Brook Trout

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**Abstract.**—There is still much to do in developing informed policy on the issue of migratory (“coaster”) brook trout *Salvelinus fontinalis*. My purpose in this paper is to provide a summary of research from other programs that may be useful for understanding the dichotomy between coaster and stream-resident brook trout. Great Lakes glacial history, population structure at the watershed level, landscape-scale habitat patterns, the energetics of resident and migratory brook trout, and dichotomous movements of young of year all provide important context for coaster brook trout. I apply a new growth model to literature sources on brook trout life history to scope the potential range of coaster–resident life histories. The results indicate that juvenile growth falls largely into two groups, depending on whether the adult prey field incorporates fish in the diet. Combining ideas on variation in the standard metabolic rate and habitat productivity with a new theory of food web structure from other authors leads to an interesting working hypothesis for coaster brook trout that builds on W. E. Ricker’s original observations on brook trout diet over 75 years ago.

Few fish species can match the breadth of life history variation of brook trout *Salvelinus fontinalis* and the range of landscapes they occupy. Brook trout range in size, growth, and maturation from small fish in coastal streams (mature at <15 cm; Hutchings 1993) to large fish in large lake and river ecosystems ( $\geq 50$  cm; Flick 1977; Castonguay et al. 1982; Quinn et al. 1994; Fraser et al. 2004). The northern distribution of the species includes anadromous populations in Boreal Shield watersheds (Dutil and Power 1980), while the southern distribution is defined by stream populations of the southern Appalachian Mountains (Habera and Moore 2005). Movements within watersheds and estuaries can be complex and highly variable (Power 1980; Lenormand et al. 2004).

The perimeter boundary of the species range in eastern North America is largely intact. Still, local and regional losses of populations through factors such as species introductions, climate change, and land use practices ought to raise concern regarding the conservation of native brook trout. Retaining the many forms and habitats of brook trout will require an understanding of the factors that generate the wide variation in life history and habitat distribution. This has important implications for the conservation of brook trout in general. More specifically, in the case of coaster brook trout in Lake Superior, addressing variation in life

history and habitat distribution has significant policy implications.

A coaster is a large form of brook trout that lives in close proximity to coastal habitat in Lake Superior. The coaster life history follows a general pattern of spawning in Lake Superior tributaries, rearing for some period of time as juveniles in stream environments, migrating out of natal streams, maturing in Lake Superior where they adopt a silver coloration and, finally, returning to tributaries for spawning. Coaster brook trout mature at larger sizes than conspecifics that remain in Lake Superior tributaries. The tendency of these brook trout to remain close to the nearshore habitat of Lake Superior provides the basis for the name “coaster.” Angling exploitation along the coast and habitat alterations in natal rivers have resulted in a greatly reduced frequency of coaster brook trout in Lake Superior watersheds (Newman et al. 2003). Coaster brook trout are now the focus of management efforts at conserving existing populations and restoring others (Newman et al. 2003). Unfortunately, historical and current information on coaster and resident brook trout are sparse.

This lack of information can be an obstacle for restoration and conservation if we view coasters as a phenomenon restricted to Lake Superior. In this situation, all policy options, including hatchery production of fish (“grow our way out of the problem”), are on the table. Although more theoretical and empirical work needs to be done, a great deal is known about brook trout ecology. This body of work is relevant for policies promoting restoration and conservation of coasters or, indeed, brook trout in general.

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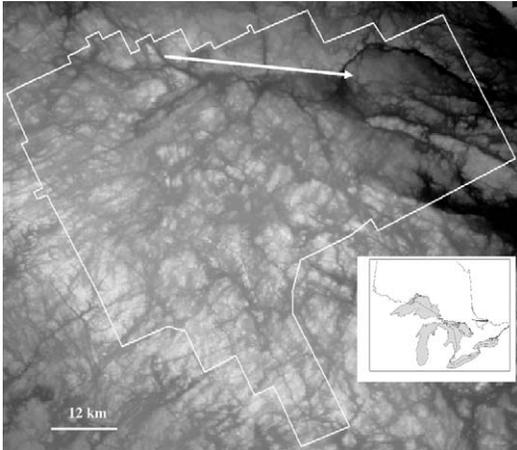


FIGURE 1.—A digital elevation map of Algonquin Park, Ontario. The white line indicates the boundaries of the park; the lighter gray areas represent higher elevations and the darker gray areas lower elevations. The postglacial drainage route can be seen near the northern boundary of the park, an arrow indicating the direction of flow. The inset shows the general location of Algonquin Park; the arrow indicates the Fossmill outlet.

Stasis should not be a policy option for brook trout conservation.

While coasters are viewed as restricted to the watersheds and coast of Lake Superior (Newman et al. 2003), it is important to recall that brook trout conservation in Great Lakes tributaries is a general issue (Steedman 1988; Danzmann et al. 1998). Large-bodied brook trout are not restricted to Lake Superior alone, but are found in many locations throughout their native range. Coasters and their stream-resident counterparts are not unique in defining the limits of brook trout size and life history. In addition, many tributaries, including Lake Superior tributaries, do not produce coaster brook trout, but retain resident brook trout.

I outline ideas stemming from different research programs that will hopefully provide some new perspectives on scientific priorities and policy development for coasters. My ideas fall into two general categories based on available literature. First, brook trout distribution (postglacial movements in the Great Lakes; population structure at watershed scales; seepage habitat frequency scaling with watershed size) and movements (phenotypic difference in metabolic rate between anadromous and resident fish; individual variation in foraging mode) are key factors in addressing the coaster phenomenon. Second, general insights into the life history variation of coasters can be gained through application of new theory to existing brook

trout life history data. When these ideas are considered collectively, I maintain that phenotypic variation in standard metabolic rate and growth efficiencies ought to be related to movement dynamics at watershed scales. Finally, I propose an extension to recent theoretical and empirical insights on food web stability (Rooney et al. 2006) to suggest that resident-coaster dichotomy maps onto ecosystem “energy channels”—an interpretation designed to produce a shift in hypotheses for coaster ecology and management.

### History Matters: Great Lakes Drainage Patterns and Postglacial Distribution

Regarding coaster brook trout as only a Lake Superior phenomenon emphasizes current distribution patterns without regard to past postglacial distribution during the formation of the Great Lakes. There is a strong possibility that coaster and resident forms of brook trout existed in periglacial drainage areas after dispersal of brook trout from the Atlantic refugium (Mandrak and Crossman 1992). The period 12,000–9,000 years before the present (BP) represented a shift in the drainage of melting glacial waters of the proto-Great Lakes from a predominantly southerly direction to the easterly direction recognizable today (Bailey and Smith 1981; Mandrak and Crossman 1992). During this period, drainage from Lakes Duluth (proto-Lake Superior) and Algonquin (proto-Lakes Michigan and Huron) changed to an easterly direction through early Lake Nipissing and the Fossmill outlet and on through what is now recognized as the Ottawa River (Figure 1; Bailey and Smith 1981; Mandrak and Crossman 1992). Isostatic rebound closed the easterly drainage systems approximately 6,000 years BP (Bailey and Smith 1981), leading to the current drainage patterns of the Great Lakes.

Figure 1 is a digital elevation map of the Algonquin Park area in southern Ontario, where the Fossmill outlet of the postglacial Great Lakes can be clearly detected at the northern end of the park. This area probably supported resident and migratory forms of brook trout in what were then tributaries of the early Great Lakes. Now, descendants of these brook trout are residents of lakes and streams with no access to the Great Lakes. Their phenotypic variation covers the range in body size currently observed in coaster watersheds of Lake Superior (e.g., Quinn et al. 1994).

### Watersheds and Brook Trout Diversity

The genetic diversity of brook trout reflects the postglacial history of eastern North America quite well, including the Great Lakes region (Danzmann et al. 1998; Castric and Bernatchez 2003). Surveys of brook trout population structure and genetic diversity among

and within watersheds have important implications for coaster brook trout.

First, and most fundamentally, the interplay of history and local ecology drives genetic diversity among brook trout populations (Fraser and Bernatchez 2008). Genetic differentiation among watersheds is relatively low compared with within-watershed population structuring (Castric et al. 2001). However, within populations, measures of genetic diversity are not related to habitat size for either lake (Angers et al. 1999) or river ecosystems (Hébert et al. 2000). River systems show higher genetic diversity within populations than do lakes, suggesting the presence of metapopulations with genetic exchange among fish within the watershed (Hébert et al. 2000). The multisite comparison of genetic diversity in coastal brook trout populations by Castric and Bernatchez (2003) is particularly instructive. They found high levels of genetic diversity within watersheds and genetically distinct populations among watersheds. Isolation by distance could not account for this pattern. They reasoned that founder effects based on relatively few fish establishing new populations are potentially a significant factor in setting population structure during postglacial expansion of brook trout.

Second, there is greater genetic similarity between the resident and anadromous forms of brook trout within watersheds than among watersheds (Jones et al. 1997), including Lake Superior watersheds with resident and coaster forms (D'Amelio and Wilson 2008, this issue). Within very large lake and river watersheds, genetic structure of different spawning populations reveals double-invasion episodes by brook trout in the postglacial period (Fraser and Bernatchez 2005). Within large watershed systems, population structuring among separate breeding populations is driven by asymmetric gene flow from sites with high effective population size ( $N_e$ ) to sites with low effective population size and largely by sex-biased dispersal (Fraser et al. 2004). A number of conclusions can be drawn with respect to coaster brook trout in Lake Superior. First, any approach for conserving genetic diversity and population structure of brook trout needs to operate conceptually at the watershed scale rather than with a purely traditional approach emphasizing geographic distance among populations. Second, resident and migratory forms of brook trout within a watershed probably have a common history and genetic similarity. Third, ecological processes within watersheds are probably important in generating the life history differences we find within watersheds.

#### Lake Size and Scale

An interesting feature of brook trout ecology in lake ecosystems has emerged at landscape scales that may

be relevant for coaster brook trout ecology (Borwick et al. 2006). The frequency (sites per kilometer of shore) of young-of-year (hereafter, age-0) brook trout habitat (seeps and streams along the shoreline) in the land-lake ecotone declines with increasing lake surface area. The decline in habitat frequency with lake size was not described by either fractal or geometric models (expanding circumference of a lake perimeter with increasing lake surface area) of potential habitat frequency. The decline in habitat along lakeshores appeared to be the result of the increasing branching structure of stream networks that occur in larger lake basins relative to those in smaller basins. In small lake basins, small streams and seeps are not part of larger stream networks, and the subwatersheds that define these habitats are more likely to drain directly into the lake. The presence of these subwatersheds is not detectable at most map scales employed by resource management agencies. Topographic indexes were used to detect seepage habitat (Borwick et al. 2006).

There are a number of implications for coaster brook trout in Lake Superior watersheds if habitat is part of any restoration effort (Newman et al. 2003). This is especially true if the scale of age-0 brook trout habitat in streams and rivers follows a similar pattern as found with lake surface area outlined above; that is, the frequency of seepage habitat declines with increasing watershed size. First, the seepage habitat of age-0 brook trout could represent a very small proportion of all available habitats. Second, habitat for both resident and age-0 coasters is likely to occur at scales below the map resolution of Lake Superior watersheds. Third, smaller watersheds may have proportionately more age-0 habitat, but this may not be related to stream productivity and, ultimately, the presence of coasters within the watershed. Fourth, fine-scale habitat where young brook trout reside may be numerous for larger watersheds, but may not occur in the main river. Very few of the age-0 brook trout habitat sites described in Borwick et al. (2006) were associated with known spawning grounds.

#### Standard Metabolic Rate (SMR) and the Cost of Living

The use of isotopes provides a means of calibrating consumption rates relative to growth rates ( $^{137}\text{Cs}$  mass balance method) and for locating foraging locations in ecosystems ( $\delta^{13}\text{C}$  depletion). This approach provides two important insights into the bioenergetics of young brook trout that are relevant for coasters in Lake Superior. First, brook trout possess high growth efficiencies and, therefore, require a low maintenance ration (Tucker and Rasmussen 1999). The activity multiplier necessary to achieve maximum growth

efficiencies for brook trout is only 1.3–1.7 times the standard metabolic rate, the lowest activity multiplier observed for any endothermic or ectothermic vertebrate (Tucker and Rasmussen 1999). Second, young anadromous brook trout consume 1.4 times as much food as stream-resident brook trout in the year preceding movement to sea, yet anadromous and stream-resident brook trout have similar growth rates (Morinville and Rasmussen 2003). This is because anadromous brook trout have lower growth efficiencies stemming from higher metabolic costs, which is probably because of their use of faster currents for feeding relative to stream-resident brook trout (Morinville and Rasmussen 2003). Variation in metabolic rate appears to be an important phenotypic trait in brook trout that has direct fitness consequences for their life history.

Morinville and Rasmussen (2006) demonstrate that migrant brook trout occupy faster currents than resident brook trout, and that a greater range of current velocities in streams are occupied by brook trout when migrants and residents co-occur. Differences in energy allocation and habitat occupancy occurred early in life for migrant and resident brook trout. Morinville and Rasmussen (2006) hypothesized that differences in SMRs among brook trout and corresponding demands on matching habitat selection to meet physiological requirements point to potential differences in life history between the two forms. On one hand, higher growth efficiencies of resident brook trout allow them to meet their food requirements in lower-velocity habitats and with less associated costs, while migrants, on the other hand, require faster food delivery or more productive habitats to meet their requirements because of relatively poor growth efficiencies. Access to locations that provide greater profitability for migrants will ensure their persistence in the watershed and the continued presence of this phenotype in the population. The relevance of Morinville and Rasmussen's (2006) hypothesis for coaster brook trout cannot be overstated. The SMR–habitat matching hypothesis points to the spatial separation of phenotypes (i.e., the presence of migrants) if larger-scale movements are required by fish possessing higher metabolic rates and lower growth efficiencies. This has important implications for coaster brook trout based on recent theory linking migration and the ideal free distribution for foragers. Habitat matching characteristic of an ideal free distribution can occur when no individuals migrate to a habitat with a lower payoff (resource profitability) than the habitat they left (Cressman and Krivan 2006).

#### **Active versus Sit-and-Wait Foraging**

Two general movement patterns among age-0 brook trout are revealed through extended observations of

individual fish in stream and lake ecosystems (Grant and Noakes 1987; McLaughlin et al. 1992, 1999; Biro and Ridgway 1995; McLaughlin 2001). Some fish remain relatively sedentary in their foraging location and feed on the bottom or on subsurface prey, while others frequently move their foraging location and remain active in prey pursuit primarily in the upper water column and at the surface. Actively foraging age-0 brook trout in lakes and streams have higher forage attempt rates but lower prey ingestion rates relative to fish employing the sit-and-wait tactic (Biro et al. 1996; McLaughlin et al. 2000). The growth rate potential (measured as RNA tissue concentration) for age-0 brook trout was highest for sit-and-wait fish and active fish and lower for fish with intermediate levels of foraging activity (McLaughlin et al. 1999). The lower ingestion rate for actively foraging age-0 brook trout suggests lower growth efficiency because of the potentially higher costs of foraging (i.e., lower food intake rate relative to energy expenditures versus sit-and-wait fish). Currently, there are no data linking the differences in growth efficiency between stream-resident and migratory forms of brook trout (Tucker and Rasmussen 1999; Morinville and Rasmussen 2003; Thériault and Dodson 2003) with the results comparing sit-and-wait versus active-foraging age-0 brook trout (e.g., McLaughlin et al. 1999). However, if a link did exist, then migrant and resident brook trout could be detected in the field during the age-0 stage, facilitating research on habitat use and distribution.

#### **Life History Variation**

Data on life history variation between coaster and resident brook trout are sparse, representing one of the most important gaps in our understanding of the ecology and evolution of coasters. Until that gap is filled, a comparative approach to understanding brook trout life history variation is needed based on data from other populations. This is possible because of two fundamental phases of growth in fish. One is represented by a period of energy allocation to somatic growth before maturation and the other is represented by a period after maturation defined by a trade-off between somatic growth and reproduction. A biphasic von Bertalanffy growth model that recognizes differences in growth before and after maturation was used to compare growth and life history variation among a set of brook trout populations (Lester et al. 2004; Shuter et al. 2005). The background and life history model description as applied to a brook trout data set is outlined in the appendix.

Wide variation in size at age defines brook trout growth among populations, maximum age ranging from 4 to over 11 years in Sierra Nevada streams of California (Hall 1991; Figure 2). In particular, the size

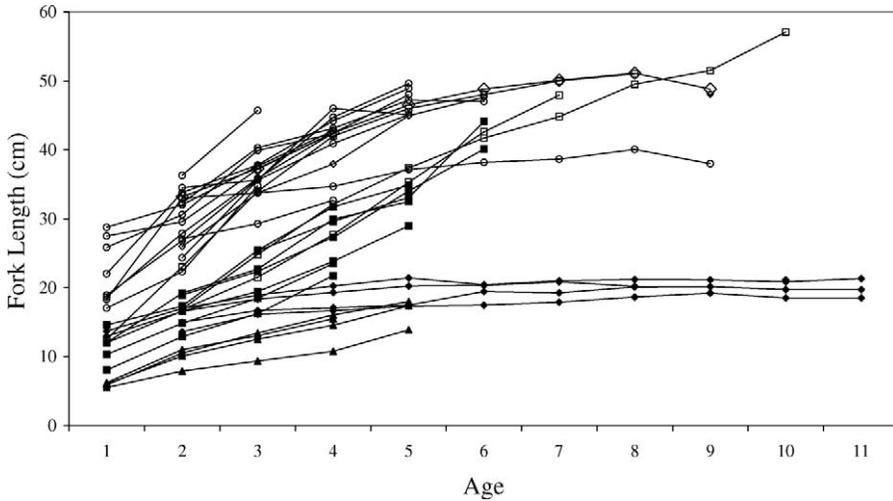


FIGURE 2.—Length at age for brook trout from the population set used in the life history comparison. Data sources are as follows: triangles, Hutchings (1990); filled diamonds, Hall (1991); filled squares, Wiseman (1969); open squares, Dutil and Power (1980) and Castonguay et al. (1982); circles, Quinn et al. (1994) and Mykiss Lake data; and open diamonds, Malette (1993).

of anadromous and resident Sutton River brook trout (Figure 2) are within the size range observed for Algonquin Park brook trout (Figure 2) residing in smaller lake ecosystems (25- to 600-ha surface area). The size variation observed in this data set appears to cover the range associated with Lake Superior coasters (11.3 cm at age 1, 21.5 cm at age 2, 35.1 cm at age 3, and approximately 50 cm at maximum length ( $L_{max}$ ); information from Isle Royale and Nipigon River combined; Newman and Dubois 1996).

Plotting juvenile growth ( $h$ ; cm/year) shows that it has a nonnormal distribution among populations (Figure 3), an interesting result that is not immediately apparent in the size-at-age data. Reports of diet for brook trout in each population (when available) provide an insight into the dichotomy in juvenile growth rate based on prey field. Brook trout populations with fish in their diet as adults are represented by populations with juvenile growth ( $h > 7.0$  cm/year), while populations without fish in their diet as adults have a juvenile growth of less than 7.0 cm/year. The available data on coaster size at age indicate that juvenile growth is 9.65 cm. Two sites in this data set are represented by both resident and anadromous forms (Sutton River, Ontario [Malette 1993]; Indian River, Newfoundland [Wiseman 1969]). For anadromous and resident brook trout from the Sutton River, juvenile growth was above 7.0 cm/year (Sutton River anadromous:  $h = 15.5$  cm/year; Sutton River resident:  $h = 11.87$  cm/year). In the Indian River, growth of anadromous juveniles was above 7.0 cm/year and

juvenile growth for the resident population was below this benchmark (Indian River anadromous:  $h = 7.9$  cm/year; Indian River resident:  $h = 5.35$  cm/year). The resident form of brook trout in the Indian River did not have fish in their diet (Wiseman 1969). Populations in the lower mode (2–6 cm/year; Figure 3) are reported to consume invertebrates and insects only.

Populations of brook trout are sometimes described as spawning at a particular age (e.g., age at maturation [ $T$ ];  $T + 1 =$  age 3), leaving maturity at age 2. Populations in this analysis were described as maturing within an age range (e.g., ages 1–3; Hall 1991). Others provide a fixed size at maturity for a set of populations

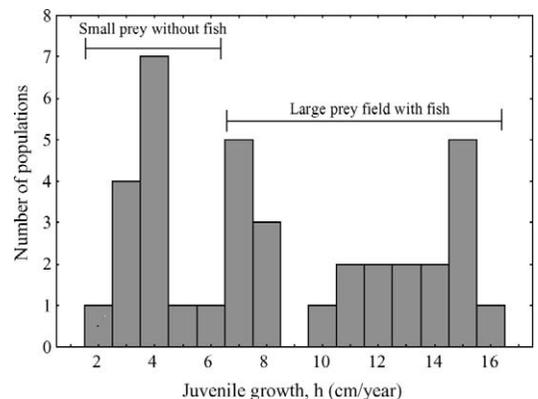


FIGURE 3.—The distribution of juvenile growth among the brook trout in the population data set. Populations with and without fish in the adult diet are distinguished.

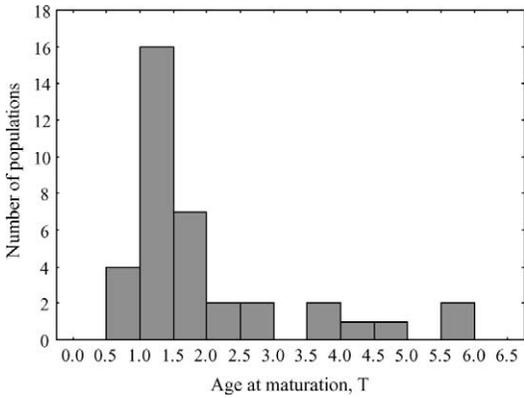


FIGURE 4.—Age at maturation for the brook trout populations used in the analysis of life history variation.

(e.g., 28 cm; Quinn et al. 1994). Still, others did not collect maturity information. Based on the biphasic von Bertalanffy growth model,  $T$  ranged from less than 1 year to age 5 (Figure 4). Generally, most brook trout populations used in this analysis appear to be maturing between 1 and 2 years of age. With a maximum size of 50.5 cm (~10% above mean size for spawning for Nipigon River females; Newman and DuBois 1996) and a maximum age of 8 years, the age of maturation for coasters is 1.56 years, well within the most common pattern for age of maturation for brook trout (Figure 4).

The results for the assumption of a common maturity and spawning age ( $T$  and  $T + 1 =$  age 3) show a clear bias in the model length at age 3 relative to the observed length at age 3 (Figure 5a). When population-specific estimates of  $T$  are used, there is much better agreement between model and observed lengths at age 3, although some bias remains, the model tending to underestimate length at age 3 (Figure 5b). Still, the fit between model and observed lengths at age 3 is improved. The comparison demonstrates that an assumed common age of maturity that is older than the actual age at maturity generates lower size-at-age estimates in the model because lower growth rates occurring at the start of the adult phase are incorporated into estimates of juvenile growth.

Estimates of reproductive investment,  $g$ , were found by adjusting this parameter in the biphasic growth model so that the observed and model lengths at spawning matched. Reproductive investment ranged from 0.32 to 1.25 with a mean of 0.75 (Figure 6). Most estimates of  $g$  in this analysis are higher than gonadosomatic index (GSI) ratios reported in the source studies. For example, GSI for Sutton River anadromous fish is 0.55 (here,  $g = 0.6$ ), while resident

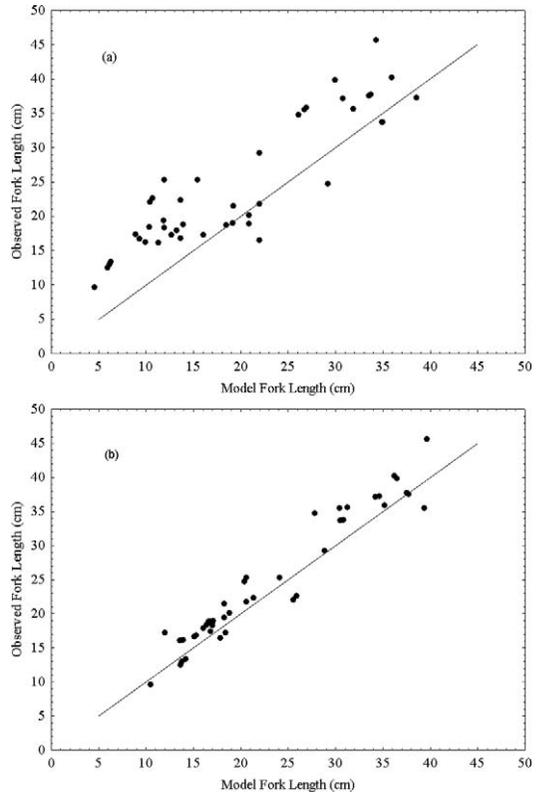


FIGURE 5.—Relationships between model length at age 3 and observed length at age 3 for anadromous and stream-resident brook trout. The diagonal lines denote 1:1 relationships. In panel (a) all populations are assumed to mature and spawn at age 3; in panel (b) all populations mature at population-specific ages of maturation based on the data in Figure 6. The reproductive investment parameter ( $g$ ) was not adjusted to provide a fit between the model and observed lengths.

brook trout in the Sutton River have a GSI of 0.35 (here,  $g = 0.57$ ; Malette 1993). In small coastal streams of Newfoundland, GSI was generally in the range of 0.1–0.2 (Hutchings 1996), but  $g$  ranged from 0.7 to 1.0 in this analysis. An estimate of  $g$  for coaster brook trout is well within the general pattern ( $g = 0.6$ ). The parameter  $g$  in the biphasic von Bertalanffy growth model includes reproductive investment in gonad production as well as in other activities, such as migration or site preparation. The competitive mating system of brook trout includes anadromous migration in some populations as well as site preparation and defense from competitors (Blanchfield and Ridgway 1997, 2005), so any estimate of  $g$  may, indeed, exceed a GSI estimate. In comparisons among lake trout *S. namaycush*, cisco *Coregonus artedii*, walleye *Sander vitreus*, and yellow perch *Perca flavescens*, GSI and

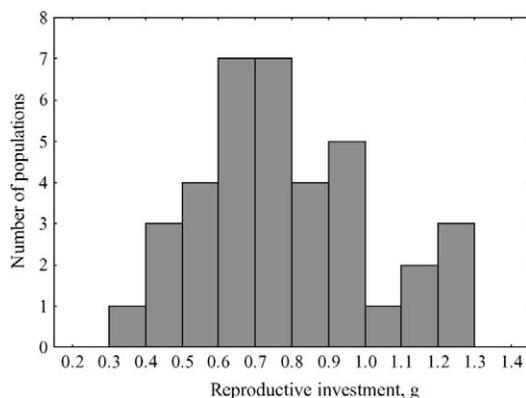


FIGURE 6.—Reproductive investment ( $g$ ) for brook trout females in the populations studied. The estimates of  $g$  were derived by adjusting this parameter so that model lengths at spawning matched the observed lengths at spawning age. Spawning occurs at age 3 for all populations except those in high-elevation California lakes, for which it occurs at age 5. Population-specific maturation is based on the data in Figure 7.

estimates of  $g$  were similar after adjusting  $g$  so that the observed and model lengths at age matched (Shuter et al. 2005). The absence of strong secondary sexual characters, lack of site preparation, and the general noncompetitive mating systems of these four species may account for the differences between this group of species and brook trout.

One interesting outcome of adjusting  $g$  to match model and observed size at spawning is that some estimates of reproductive investment equal or exceed 1.0 (Figure 6). This implies that a female's annual reproductive investment, as a proportion of somatic weight that is energetically equivalent to investment in gonads and other reproductive investment, exceeds that allocated to growth and maintenance. In part, this may reflect a number of issues, such as age interpretation, the growth models used to develop observed size at age, or the sample size used to estimate maximum length of fish. On the other hand, some studies report a decline in fecundity with age and indicate that senescence is detectable in the condition of older mature fish (e.g., Hall 1991).

The life history invariant,  $Z/k$  (where  $Z$  is instantaneous mortality and  $k$  is the von Bertalanffy growth coefficient) was used to confirm whether the parameters in this analysis were within acceptable limits, considering the diversity of literature sources used in this study. The mean of  $Z/k$  (2.715) fell within the expected range (2.6–4.5), some populations falling above and below the expected range ( $N = 37$ ; 95% confidence interval = 2.48–2.96; range = 1.79–5.40). In general,

the parameters of the biphasic growth model derived from information on basic size at age, maximum age, and maximum size provided reasonable life history patterns. Based on information from Newman and Dubois (1996),  $Z/k = 3.0$  for coaster brook trout.

Finally, the relationship between the length of young spawning brook trout (age 3 for most populations, age 5 for the populations in Hall 1991) as a function of juvenile growth,  $h$ , was estimated with a linear model (Figure 7; length =  $7.476 + 2.113h$ ; SE of intercept = 1.293; SE of slope = 0.130;  $R^2 = 0.88$ ). The anadromous and resident brook trout of the Sutton and Indian rivers are highlighted (Figure 7). The cluster of sites in the vicinity of the Sutton River anadromous and resident data in Figure 7 are all from lakes in Algonquin Park (20- to 600-ha surface area), where there is no lake–river migration. Large size in brook trout can occur in migratory and nonmigratory populations.

The first empirical confirmation of the biphasic growth model used precise measures of maturity, gonadosomatic ratio, and maximum age based on large sample sizes (Shuter et al. 2005). This level of detail was not available for all of the brook trout populations used in this analysis. This is typical for literature-based data on life history. For example, age at spawning is routinely equated with age at maturation, and spawning age is normally provided as a single age (commonly age 3 in brook trout). Small sample sizes probably miss the few fish showing maximum age, as in the summary of Algonquin Park brook trout (Quinn et al. 1994). Juvenile size is either based on direct estimates from samples of young fish or by back-calculation methods that may or may not account for traditional biases using different growth and intercept models. With all these considerations in mind, it is interesting to see patterns emerge in brook trout life history variation. Specifically, populations that include fish in their diet as adults relative to those with only benthic invertebrates and aquatic insects in the adult diet appear to have values of  $h$  that fall into two groups. The role of fish in extending the prey field of adult brook trout beyond invertebrates and, ultimately, their maximum length, was first noted by Ricker (1930) over 75 years ago. Ricker (1930) discussed the similarity of diet among populations during their juvenile period (primarily benthic invertebrates and aquatic insects) and the divergence in size that occurs among populations based on whether or not adult brook trout are able to acquire fish in their diet.

#### Energy Channels and the Spatial Distribution of Brook Trout Phenotypes in Ecosystems

The divergence in size noted by Ricker (1930), and confirmed by patterns in life history variation based on prey field (presence or absence of fish in diet), point to an

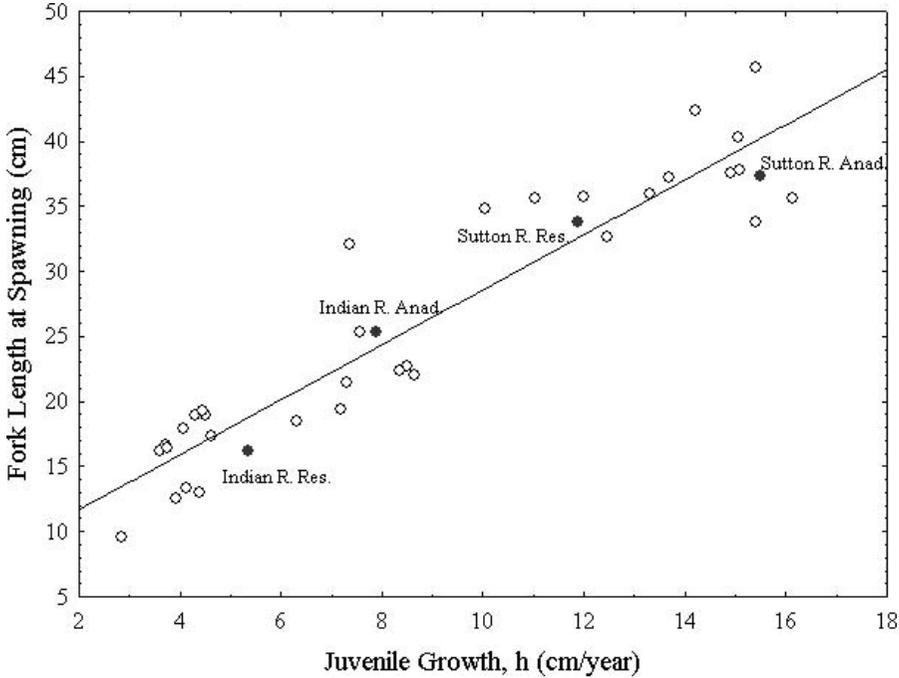


FIGURE 7.—Relationship between juvenile growth in brook trout and size at spawning (age 3 or 5) for each population. Data for sites with both anadromous (Anad) and resident (Res) populations are indicated by solid circles for the Indian (Wiseman 1969) and Sutton (Malette 1993) rivers. Open circles represent all other populations in the data set.

interesting application of recent theory and evidence on the stability and structure of food webs. Rooney et al. (2006) showed that mobile top predators structure and couple food webs through consumption of prey supported by distinct energy channels (carbon sources) described as fast (e.g., phytoplankton production) and slow (e.g., detritus decomposition). Food webs are asymmetric; peaks in trophic positions are higher for predators when linked to energy channels with faster turnover rates in basal resources relative to channels with slower turnover rates (Rooney et al. 2006). Lower trophic positions of predators are associated with slower energy channels. The Rooney et al. (2006) analysis demonstrates that asynchronies in energy flow can stabilize food web interactions within an ecosystem (e.g., a lake). It is possible to consider a variation of the Rooney et al. (2006) proposal for asymmetric energy flow within an ecosystem to a situation where individuals *within* a population occupy either fast or slow energy flows *between* ecosystems by building on the ideas of Morinville and Rasmussen (2006), Rooney et al. (2006), and life history variation with and without large prey fields to account for the coaster–resident dichotomy.

The basis of this hypothesis is that phenotypic variation in SMR exists in brook trout populations and results in a range of unequal competitors (Morinville

and Rasmussen 2003, 2006). The energetic scope of brook trout stemming from their low field metabolic rate results in fish with low SMR (residents) and high growth efficiencies remaining in relatively unproductive habitats. In contrast, fish with relatively higher SMR (coasters or migrants) and low growth efficiencies cannot sustain profitable foraging in unproductive habitats. As noted by Morinville and Rasmussen (2006), the energetic scope of resident brook trout may be limited, but individuals are able to live in profitable (yet unproductive) habitats, given the efficiency of their phenotypes. On the other hand, migrants must find a match between their relatively inefficient phenotypes and habitat productivity. They must move from a habitat with a low payoff to a habitat with a higher payoff. They can meet this requirement through greater movements and wider criteria for habitat selection (i.e., faster currents, perhaps) at age 0 and, ultimately, at larger scales during adult maturation. In theory, so long as age-0 brook trout migrate to habitats with higher payoffs for fitness and not to habitats with lower payoffs, then an ideal free distribution of brook trout may emerge at larger watershed scales (Cressman and Krivan 2006). The manifestation of this phenotypic diversity and movement by some to more productive habitats is what we

observe as resident and coaster brook trout at the watershed scale. Ultimately, fish with higher SMR will confront unproductive habitats and a truncated prey field sooner than resident fish, which may be the basis for so-called size thresholds in migration found in anadromous brook trout populations (e.g., Thériault and Dodson 2003). The influence of environmental variation on phenotypic expression (as described here) represents reaction norms within watersheds.

The ecosystem context of this hypothesis is intriguing. The spatial distribution of brook trout phenotypes, such as the coaster–resident dichotomy, can be represented by a schematic diagram of asymmetric food web structure based on Rooney et al. (2006; Figure 8). The trophic position of brook trout shifts from a low level in unproductive habitats, such as small headwater streams of resident brook trout, to higher trophic positions for individuals moving to more productive habitats, such as lakes (Figure 8). Coaster or anadromous brook trout essentially move to energy channels with faster turnover rates, resulting in higher trophic positions through a process of matching SMR to habitat productivity. Larger-scale movements and eventual incorporation of larger prey fields (i.e., fish prey) result in higher growth rates as migrant brook trout finally achieve growth efficiencies stemming from pursuing larger but less costly prey fields (see Pazzia et al. 2002).

Taking this hypothesis a step further, access (or the lack thereof) to environments with relatively fast turnover of basal resources plays a role in selection for phenotypes in brook trout populations. The presence of fast-growing lake-based populations of brook trout in areas of the historic Great Lakes drainages, such as Algonquin Park in Ontario (Figure 7) or the Adirondack Mountains of New York, could represent a loss of efficient, low SMR phenotypes as lake environments select for fish able to succeed in fast energy channels (Figure 8). In other locations, selection may have favored more efficient phenotypes at the expense of other phenotypes if brook trout lacked access to productive environments and remained in slow energy channels. This may explain the occurrence of small forms of brook trout in isolated streams. Finally, a wide range of phenotypes could be retained in watersheds if access to fast (lakes or estuaries) and slow (headwater streams) energy channels remains. The case of coaster and resident brook trout may follow this scenario.

### Summary

The absence of genetic differentiation between sympatric groups with different life histories is

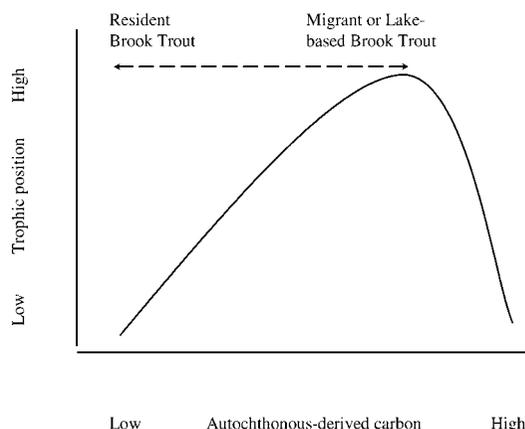


FIGURE 8.—Schematic diagram illustrating the hypothesis that different energy channels and relative trophic positions characterize brook trout resident in streams and those that migrate to lakes; the diagram is based on an analysis by Rooney et al. (2006) of food web stability within ecosystems. The asymmetry derives from faster turnover rates in basal resources for one energy channel than other channels. Low autochthonous-derived carbon could result from the detritus processing that occurs in small streams (slow energy channel), while high autochthonous-derived carbon could result from fish prey consumed by migrant brook trout or brook trout residing in lakes (fast energy channel). Populations of brook trout are composed of different phenotypes based on their standard metabolic rates—and therefore trophic positions—depending on their access to and the mixing of energy channels. The metabolic scope of brook trout allows individual phenotypes to persist by either remaining in slow energy channels (small streams) or moving to faster energy channels (lakes) in ecosystems if spatial access is available. Lack of access to slow or fast energy channels will select against different phenotypes.

common within salmonid species (see Heath et al. 2008). Because stream and resident coaster brook trout within a watershed cannot be distinguished by microsatellite loci (D'Amelio and Wilson, in press), we cannot take refuge in traditional approaches by regarding them as separate stocks. The purpose of this set of papers and this synthesis is to highlight current science and draw on other research programs to inform us about the coaster phenomenon. Together, this work provides a more comprehensive view of brook trout ecology and life history that can better inform research and policy development, despite relatively sparse information on coaster brook trout in Lake Superior.

Why are coasters absent while stream-resident brook trout are present and widely distributed in Lake Superior watersheds? Overexploitation of coasters could have resulted in selection against this phenotype in watersheds, leaving only resident fish. Habitat changes in streams and rivers may have resulted in

losses of productive habitat for brook trout that required this rearing habitat before moving to Lake Superior to complete maturation. Perhaps more importantly, the introduction of nonnative salmonines in Lake Superior has resulted in competitive exclusion of brook trout phenotypes that must compete with other active salmonine species for rearing habitat, leaving only resident forms that can effectively exploit a relatively unproductive system. Whatever the mechanism associated with the decline of coasters in different Lake Superior watersheds, the recovery and conservation of this form of brook trout will require some new research and policy directions. Certainly, watershed-based policies are needed since large forms of brook trout are possibly products of fast energy channels in ecosystems, either through spatially explicit food webs (e.g., residency versus migration) or within food webs that are largely driven by fast energy channels (e.g., lakes). Understanding just what can be achieved in the restoration of coasters in light of the food web changes associated with other salmonines in Lake Superior is another area for research and policy analysis.

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### References

- Angers, B., P. Magnan, M. Plante, and L. Bernatchez. 1999. Canonical correspondence analysis for estimating spatial and environmental effects on microsatellite gene diversity in brook charr (*Salvelinus fontinalis*). *Molecular Ecology* 8:1043–1053.
- Bailey, R. M., and G. R. Smith. 1981. Origin and geography of the fish fauna of the Laurentian Great Lakes basin. *Canadian Journal of Fisheries and Aquatic Sciences* 38:1539–1561.
- Biro, P. A., and M. S. Ridgway. 1995. Individual variation in foraging movements in a lake population of young-of-year brook charr (*Salvelinus fontinalis*). *Behaviour* 132:57–74.
- Biro, P. A., M. S. Ridgway, and R. L. McLaughlin. 1996. Does the rate of foraging attempts predict ingestion rate for young-of-the-year brook trout (*Salvelinus fontinalis*) in the field? *Canadian Journal of Fisheries and Aquatic Sciences* 53:1814–1820.
- Blanchfield, P. J., and M. S. Ridgway. 1997. Reproductive timing and use of redd sites by lake-spawning brook trout (*Salvelinus fontinalis*). *Canadian Journal of Fisheries and Aquatic Sciences* 54:747–756.
- Blanchfield, P. J., and M. S. Ridgway. 2005. The relative influence of breeding competition and habitat quality on female reproductive success in lacustrine brook trout (*Salvelinus fontinalis*). *Canadian Journal of Fisheries and Aquatic Sciences* 62:2694–2705.
- Borwick, J., J. Buttle, and M. S. Ridgway. 2006. A topographic index approach for identifying groundwater habitat of young-of-year brook trout in the land–lake ecotone. *Canadian Journal of Fisheries and Aquatic Sciences* 63:239–253.
- Castonguay, M., G. J. FitzGerald, and Y. Coté. 1982. Life history and movements of anadromous brook charr, *Salvelinus fontinalis*, in the St-Jean River, Gaspé, Quebec. *Canadian Journal of Zoology* 60:3084–3091.
- Castric, V., and L. Bernatchez. 2003. The rise and fall of isolation by distance in the anadromous brook charr (*Salvelinus fontinalis* Mitchell). *Genetics* 163:983–996.
- Castric, V., F. Bonney, and L. Bernatchez. 2001. Landscape structure and hierarchical genetic diversity in the brook charr, *Salvelinus fontinalis*. *Evolution* 55:1016–1028.
- Charnov, E. 1993. Life history invariants: some explorations of symmetry in evolutionary ecology. Oxford University Press, Oxford, UK.
- Cressman, R., and V. Krivan. 2006. Migration dynamics for the ideal free distribution. *American Naturalist* 168:384–397.
- D'Amelio, S. D., and C. Wilson. In press. Genetic population structure among source populations for coaster brook trout in Nipigon Bay, Lake Superior. *Transactions of the American Fisheries Society*.
- Danzmann, R. G., R. P. Morgan, M. W. Jones, L. Bernatchez, and P. E. Ihssen. 1998. A major sextet of mitochondrial DNA phylogenetic assemblages extant in eastern North American brook trout (*Salvelinus fontinalis*): distribution and postglacial dispersal patterns. *Canadian Journal of Zoology* 76:1300–1318.
- Dutil, J. D., and G. Power. 1980. Coastal populations of brook trout, *Salvelinus fontinalis*, in Lac-Guillaume-Delisle (Richmond Gulf), Quebec. *Canadian Journal of Zoology* 58:1828–1835.
- Flick, W. A. 1977. Some observations on age, growth, food habits, and vulnerability of large brook trout (*Salvelinus fontinalis*) from four Canadian lakes. *Naturaliste Canadien* 104:353–359.
- Fraser, D. J., and L. Bernatchez. 2005. Allopatric origins of sympatric brook charr populations: colonization history and admixture. *Molecular Ecology* 14:1497–1509.
- Fraser, D. J., and L. Bernatchez. 2008. Ecology, evolution, and conservation of lake-migratory brook trout: a perspective from pristine populations. *Transactions of the American Fisheries Society* 137:1192–1202.
- Fraser, D. J., C. Lippé, and L. Bernatchez. 2004. Consequences of unequal population size, asymmetric gene flow, and sex-biased dispersal on population structure in brook charr (*Salvelinus fontinalis*). *Molecular Ecology* 13:67–80.
- Grant, J. W. A., and D. L. G. Noakes. 1987. Movers and stayers: foraging tactics of young-of-the-year brook charr, *Salvelinus fontinalis*. *Journal of Animal Ecology* 58:773–789.
- Habera, J., and S. Moore. 2005. Managing southern Appalachian brook trout: a position statement. *Fisheries* 30(7):10–20.

- Hall, D. L. 1991. Growth, fecundity, and recruitment responses of stunted brook trout populations to density reduction. Doctoral dissertation. University of British Columbia, Vancouver.
- Heath, D. D., C. M. Bettles, S. Jamieson, I. Stasiak, and M. F. Docker. 2008. Genetic differentiation among sympatric migratory and resident life history forms of rainbow trout in British Columbia. *Transactions of the American Fisheries Society* 137:1268–1277.
- Hébert, C., R. G. Danzman, M. W. Jones, and L. Bernatchez. 2000. Hydrography and population genetic structure in brook charr (*Salvelinus fontinalis*, Mitchell) from eastern Canada. *Molecular Ecology* 9:971–982.
- Hoenig, J. M. 1983. Empirical use of longevity data to estimate mortality rates. U.S. National Marine Fisheries Service Fishery Bulletin 82:898–903.
- Hutchings, J. A. 1990. The evolutionary significance of life history divergence among brook trout, *Salvelinus fontinalis*, populations. Doctoral dissertation. Memorial University of Newfoundland, St. Johns.
- Hutchings, J. A. 1993. Adaptive life histories affected by age-specific survival and growth. *Ecology* 74:673–684.
- Hutchings, J. A. 1996. Adaptive phenotypic plasticity in brook trout, *Salvelinus fontinalis*, life histories. *Ecoscience* 3:25–32.
- Jones, M. W., R. G. Danzmann, and D. Clay. 1997. Genetic relationships among populations of wild resident and wild and hatchery anadromous brook charr. *Journal of Fish Biology* 51:29–40.
- Lenormand, S., J. J. Dodson, and A. Menard. 2004. Seasonal and ontogenetic patterns in the migration of anadromous brook trout (*Salvelinus fontinalis*). *Canadian Journal of Fisheries and Aquatic Sciences* 61:54–67.
- Lester, N. P., B. J. Shuter, and P. A. Abrams. 2004. Interpreting the von Bertalanffy model of somatic growth in fishes: the cost of reproduction. *Proceedings of the Royal Society of London B* 271:1625–1631.
- Malette, M. D. 1993. Growth and anadromy of brook trout (*Salvelinus fontinalis* (Mitchill)) from Sutton River, Hudson Bay lowland. Master's thesis. Laurentian University, Sudbury, Ontario, Canada.
- Mandrak, N. E., and E. J. Crossman. 1992. Postglacial dispersal of freshwater fishes into Ontario. *Canadian Journal of Zoology* 70:2247–2259.
- McLaughlin, R. L. 2001. Behavioural diversification in brook charr: adaptive responses to local conditions. *Journal of Animal Ecology* 70:325–337.
- McLaughlin, R. L., M. M. Ferguson, and D. L. G. Noakes. 1999. Adaptive peaks and alternative foraging tactics in brook charr: evidence of short-term divergent selection for sitting-and-waiting and actively searching. *Behavioral Ecology and Sociobiology* 45:386–395.
- McLaughlin, R. L., J. W. A. Grant, and D. L. Kramer. 1992. Individual variation and alternative patterns of foraging movements in recently emerged brook charr (*Salvelinus fontinalis*). *Behaviour* 120:286–301.
- McLaughlin, R. L., J. W. A. Grant, and D. L. G. Noakes. 2000. Living with failure: the prey capture success of young brook charr in streams. *Ecology of Freshwater Fish* 9:81–89.
- Morinville, G. R., and J. B. Rasmussen. 2003. Early juvenile bioenergetic differences between anadromous and resident brook trout (*Salvelinus fontinalis*). *Canadian Journal of Fisheries and Aquatic Sciences* 60:401–410.
- Morinville, G. R., and J. B. Rasmussen. 2006. 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.
- Newman, L. E., and R. B. Dubois, editors. 1996. Status of brook trout in Lake Superior. Report by the Brook Trout Subcommittee to the Great Lakes Fishery Commission, Lake Superior Technical Committee, Ann Arbor, Michigan. Available: [www.glfsc.org/pubs\\_out/docs.htm](http://www.glfsc.org/pubs_out/docs.htm). (April 2005).
- Newman, L. E., R. B. Dubois, and T. N. Halpern, editors. 2003. A brook trout rehabilitation plan for Lake Superior. Great Lakes Fishery Commission, Miscellaneous Publication 2003-03, Ann Arbor, Michigan.
- Pazzia, I., M. Trudel, M. Ridgway, and J. B. Rasmussen. 2002. Influence of food web structure on the growth and bioenergetics of lake trout (*Salvelinus namaycush*). *Canadian Journal of Fisheries and Aquatic Sciences* 59:1593–1605.
- Power, G. 1980. The brook charr, *Salvelinus fontinalis*. Pages 141–203 in E. K. Balon, editor. *Charrs: salmonid fishes of the genus Salvelinus*. Dr W. Junk, The Hague, The Netherlands.
- Quinn, N. W. S., R. M. Korver, F. J. Hicks, B. P. Monroe, and R. R. Hawkins. 1994. An empirical model of lentic brook trout. *North American Journal of Fisheries Management* 14:692–709.
- Ricker, W. E. 1930. Feeding habits of speckled trout in Ontario waters. *Transactions of the American Fisheries Society* 59:256–267.
- Rooney, N., K. McCann, G. Gellner, and J. C. Moore. 2006. Structural asymmetry and the stability of diverse food webs. *Nature (London)* 442:265–269.
- Shuter, B. J., N. P. Lester, J. LaRose, C. F. Purchase, K. Vascotto, G. Morgan, N. C. Collins, and P. A. Abrams. 2005. Optimal life histories and food web position: linkages among somatic growth, reproductive investment, and mortality. *Canadian Journal of Fisheries and Aquatic Sciences* 62:738–746.
- Steedman, R. J. 1988. Modification and assessment of an index of biotic integrity to quantify stream quality in southern Ontario. *Canadian Journal of Fisheries and Aquatic Sciences* 45:492–501.
- Steele, P. O. 1986. Life history strategies of a north temperate salmonid, *Salvelinus fontinalis*, in Polar Bear Provincial Park. Doctoral dissertation. University of Western Ontario, London.
- Thériault, V., and J. J. Dodson. 2003. Body size and the adoption of a migratory tactic in brook charr. *Journal of Fish Biology* 63:1144–1159.
- Tucker, S., and J. B. Rasmussen. 1999. Using <sup>137</sup>Cs to measure and compare bioenergetic budgets of juvenile Atlantic salmon (*Salmo salar*) and brook trout (*Salvelinus fontinalis*) in the field. *Canadian Journal of Fisheries and Aquatic Sciences* 56:875–887.
- Wiseman, R. J. 1969. Some aspects of the biology of the speckled trout *Salvelinus fontinalis* (Mitchill) 1815, in the waters of insular Newfoundland. Master's thesis. Memorial University of Newfoundland, St. John's.

**Appendix: The von Bertalanffy Biphasic Growth Model and Brook Trout Life History Variation**

Lester et al. (2004) developed the biphasic von Bertalanffy growth model to describe asymptotic growth in fish as an outcome of maturation and reproductive investment. It does so by applying the standard von Bertalanffy growth model after maturation. The parameters describing reproductive investment and pre-maturation growth constitute the traditional von Bertalanffy model. The model is biphasic because somatic growth before maturation is modeled separately. Somatic growth before maturation is linear, that is,

$$L_t = h(t - t_1),$$

where  $L_t$  is length at age  $t$ ,  $h$  is growth (cm/year) during the juvenile stage, and  $t_1$  represents the effect that predation risk and prey field can have on growth before maturation. If  $t_1 = 0$ , then predators are absent and prey is abundant and in sizes that allow for smooth growth during the juvenile stage. If  $t_1 > 0$  the presence of predators reduces risky feeding and therefore growth until a critical size is reached, whereas if  $t_1 < 0$  the size range of the prey field constrains the growth of juveniles because individuals cannot find prey of a size sufficient to maintain growth.

At the age of maturation,  $T$ , energy is allocated to reproduction in addition to somatic growth, so realized growth becomes asymptotic. After maturation ( $t > T$ ), energy allocation leads to spawning a year later,  $T + 1$ . Growth for  $t > T$  is represented by the von Bertalanffy growth model

$$L_t = L_\infty [1 - e^{-k(t-t_0)}],$$

where  $L_\infty = 3h/g$ ,  $k = \log_e(1 + g/3)$ , and  $t_0 = T + \log_e[1 - g(T - t_1)/3] / \log_e(1 + g/3)$ . The parameter  $g$  represents total reproductive investment, including egg production (e.g., GSI) and investment in the forms of migration, site preparation, and defense of offspring. It is the annual investment in reproduction as a proportion of somatic weight that is energetically equivalent to gonadal production and reproductive activities. Therefore, an estimate of  $g$  will probably be larger than a traditional estimate of  $g$  based only on GSI.

The parameters of this model can also be estimated on the assumption that the adult mortality rate,  $Z$ , selects for the age of maturity and reproductive investment that maximizes reproduction (Lester et al. 2004; Shuter et al. 2005). Exact least-squares solutions to these trade-offs are (Lester et al. 2004)

$$T - t_1 = 1.95 / (e^Z - 1)$$

and

$$g = 1.18 [e^Z - (1/e^Z)],$$

where  $Z$  is determined empirically or estimated from Hoenig's (1983) relationship between  $Z$  and maximum longevity,  $T_{\max}$  ( $Z = 4.22T_{\max}^{-0.982}$ ). A regression model was used to estimate  $t_1$ , yielding  $t_1 = 0.55 - 0.033L_\infty$  ( $R^2 = 0.35$ ,  $P < 0.0001$ ; Lester et al. 2004).

The parameter values for this model were estimated in the following steps. First, I used Hoenig's (1983) equation to estimate  $Z$  as a function of the maximum age reported in each study. Second,  $T$  was estimated in two steps. Initially, the parameter  $t_1$  was estimated from the regression model given  $L_\infty$ , and since  $T - t_1 = 1.95 / (e^Z - 1)$ ,  $T$  could then be determined by difference. Third,  $h$  was based on the linear slope defining growth to age 2. Most studies report maturation at ages less than 3 or, in a number of cases, report spawning at age 3 and above and equate this age with maturation (i.e.,  $T + 1$ ). The procedure for estimating  $T$  demonstrated that almost all brook trout populations mature at ages less than 3, most between ages 1 and 2. However, one set of populations was defined by a relatively long life span,  $T_{\max}$  ranging from age 9 to age 16 (Hall 1991). Estimates of  $T$  for these populations all indicated that maturation was generally at age 3 and above, so the  $h$  for this set of populations was the linear slope defining growth during the first 4 years. Since juvenile growth is evaluated before maturation (in the neighborhood of  $T$ ; Shuter et al. 2005:741), including size at age 2 or 4 seemed reasonable in estimating  $h$ . Fourth, estimates of  $g$  and  $k$  were based on  $h$  and  $L_\infty$  (maximum length if  $L_\infty$  was not reported for a population),  $g$  being the reproductive investment value that matched model size with observed size at age (Shuter et al. 2005). Finally, the parameter  $t_0$  was calculated with estimates of  $T$  for each population. I used the biphasic growth model to estimate the length at spawning for a set of brook trout populations (typically, brook trout spawn at age 3 or older). I adjusted the reproductive investment parameter  $g$  so that model-based size at spawning matched observed size at age 3 or age 5 (Hall 1991) and then report on this final estimate of  $g$ . I also examined the assumption that maturity and spawning both occur at the same age ( $T$  and  $T + 1 = 3$ ) by comparing model length at age 3 with observed length at age 3. This assumption is compared with the fit between model length at age 3 and observed length at age 3 when population-specific values of  $T$  are employed. In this comparison,  $g$  was estimated based on  $L_\infty$  and  $h$  for each population and not adjusted to accommodate model length with observed length at age 3.

I used published accounts of life history from a number of sources to examine the scope of life history variation in brook trout, including anadromous populations. My purpose was to place coaster brook trout and stream-resident forms that may be found in Lake Superior watersheds in a wider context. My selection did not reflect all of the available data on brook trout life history but specifically covered the range of size, growth, and life span observed in this species. The populations included were from Newfoundland (Wiseman 1969; Hutchings 1990), Quebec (Dutil and Power 1980; Castonguay et al. 1982), northern Ontario (Steele 1986; Malette 1993), lakes in Algonquin Park (Quinn et al. 1994), and high alpine lakes in the Sierra Nevada of California (introduced in the mid-1900s; Hall 1991).

The anadromous population of brook trout in the Sutton River, Ontario, was separated from resident brook trout based on strontium analysis by Malette (1993), and their growth and life history summarized based on data in Appendix 1 of Malette (1993).

To provide a broad confirmation of the parameter values derived in this approach, I used a life history invariant (Charnov 1993; Shuter et al. 2005),  $Z/k$ , to assess whether or not the data set as a whole falls within acceptable limits of the biphasic growth model. In this analysis,  $Z$  is estimated from maximum age and  $k$  is estimated from juvenile growth ( $h$ ) and reproductive investment ( $g$ ). The life history invariant in the biphasic von Bertalanffy model should range between 2.6 and 4.5.