

ADAPTIVE LIFE HISTORIES EFFECTED BY AGE-SPECIFIC SURVIVAL AND GROWTH RATE¹

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Abstract. Life history data for three unexploited populations of brook trout, *Salvelinus fontinalis*, were used to test the predictions of life history theory that, relative to juveniles, (1) high adult survival favors low reproductive effort and delayed reproduction, and (2) increased juvenile growth rate favors high effort and early reproduction. Field data supported both predictions. The population having the highest adult-to-juvenile survival ratio expended the least effort, reproduced latest in life, and experienced the lowest survival cost of reproduction. Among populations a high juvenile-to-adult growth rate was associated with early reproduction, high reproductive effort, and high reproductive cost. Early reproduction was also associated with increased growth within populations.

The adaptive significance of interpopulation variation in life history was assessed by comparing the fitness, r , of observed life histories with those of potentially alternative strategies. Empirically derived fitness functions supported the hypothesis that population differences in life history were adaptive. Observed combinations of age-specific survival and fecundity were those that maximized fitness. Within populations the fitness advantages associated with reproducing early in life favored reduced age at reproduction for the fastest-growing individuals. The results are consistent with the predictions of life history theory and demonstrate empirically how survival and growth rate can independently and interactively influence life history evolution.

Key words: adaptation; brook trout; cost of reproduction; fecundity; fitness; growth rate; life history; Newfoundland; reproductive effort; *Salvelinus fontinalis*; survival.

INTRODUCTION

Life history theory predicts how organisms vary reproductive effort throughout their lives in response to environmentally and physiologically induced changes in age-specific survival and fecundity (Williams 1966, Schaffer 1974, Charlesworth and Leòn 1976). Assuming that natural selection acts on age-specific expectations of producing future offspring (Fisher 1930), patterns of covariation between reproductive effort and age at reproduction can be predicted from adult and juvenile survival rates. Increased effort and decreased age at reproduction are favored when adult survival is low relative to juvenile survival (Gadgil and Bossert 1970, Schaffer 1974). This prediction assumes that age-specific fecundity does not change with age-specific survival, and it is most appropriately tested at the population level (Charlesworth 1980; e.g., Reznick et al. 1990).

Growth rate is of major importance to life history evolution in organisms that grow throughout their lives because of its positive influence on age-specific fecundity (Shine and Schwartzkopf 1992). Once the physiologically minimum reproductive size has been attained in such organisms, an individual's maturation

strategy will be based on the relative benefits of reproducing at present (increasing the rate of gene input at a cost to future survival or fecundity, i.e., the costs of reproduction [Williams 1966, Bell and Koufopanou 1986]), or of reproducing at a larger size in the future (increasing fecundity and possibly experience at a cost of mortality between reproductive ages [Charlesworth 1980]). Life history theory has been used to predict how age-specific combinations of survival and fecundity should respond to changes in growth rate (Gadgil and Bossert 1970, Roff 1984). In addition to a trade-off between present fecundity and future survival, Schaffer (1974) considered the trade-off between present fecundity and future growth. He predicted that environments that allowed for increased growth during potentially reproductive ages should favor delayed maturity and decreased effort.

From a life history perspective, growth rate is probably best expressed separately for juveniles and adults. The predicted effects of increased juvenile growth rate, relative to adult growth rate, on reproductive effort and age at maturity can be derived from the Euler-Lotka equation

$$1 = \sum l_x m_x e^{-rx}, \quad (1)$$

where l_x represents survival from the zygote to the

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beginning of the breeding season at age x , m_x is the number of female zygotes produced by a female at age x , and r is the intrinsic rate of natural increase.

Consider the life-cycle of an annual breeder that starts breeding at age 1 yr, where m offspring are produced at each breeding attempt, s_j is the survivorship from birth to breeding at age 1, and s_a represents adult survival between breeding events. Following Cole (1954), Schaffer (1974), and Charlesworth (1980), the Euler-Lotka equation can be simplified to

$$s_a = e^r - s_j m, \quad (2)$$

which expresses the central tenet of life history theory that future adult survival is negatively associated with present fecundity (Williams 1966). If survival is directly related to growth rate (body size is positively correlated with survival in many plants and animals; references in Hutchings 1991), Eq. 2 becomes

$$a_1 g_a = e^r - a_2 g_j m, \quad (3)$$

where g_a and g_j represent adult and juvenile growth, respectively, and where a_1 and a_2 are the respective constants of proportionality between growth rate and survival. When $a_1 = a_2$,

$$g_a = e^r - g_j m. \quad (4)$$

Assuming there is a trade-off between adult growth and present fecundity, the optimal life history corresponds to the point on the trade-off boundary of an options set (Levins 1968, Partridge and Sibly 1991) at which the fitness contour, i.e., Eq. 4, is tangential. Assume that the trade-off between present fecundity and adult growth is concave with respect to the origin (Fig. 1). Rapid juvenile growth, relative to adult growth, favors increased effort, m , whereas low values of g_j select for decreased effort. Increased juvenile growth rate also results in higher fecundity earlier in life, favoring earlier age at first reproduction (Charlesworth 1980). Thus, relative to adult growth rate, increased juvenile growth rate should favor increased effort at an earlier age of first reproduction (cf. Gadgil and Bossert 1970). This prediction can be tested at the population level by comparing the life histories of populations having different ratios of adult-to-juvenile growth rate, and at the level of the individual by comparing the life histories of individuals that grew either rapidly or slowly as juveniles.

One objective of this paper was to examine the interrelationships among survival, growth rate, age at reproduction, and reproductive effort for populations of brook trout, *Salvelinus fontinalis*, a salmonid fish endemic to northeastern North America, to test the predictions of life history theory that, relative to juveniles, (1) increased adult survival favors reduced effort and delayed reproduction, and (2) increased juvenile growth rate favors increased effort and early reproduction. I considered reproductive effort to be

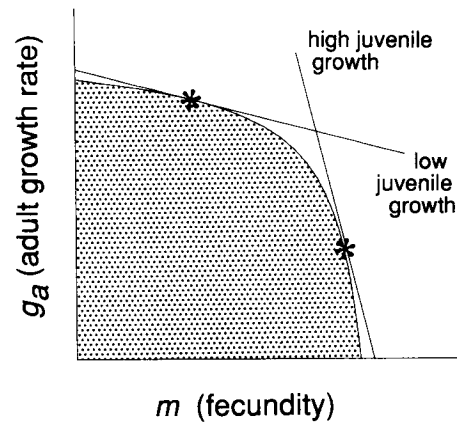


FIG. 1. Options set for combinations of present fecundity, m , and adult growth rate, g_a . Straight-line fitness functions correspond to Eq. 4 having high and low slopes, i.e., values of juvenile growth rate, g_j .

approximated by the ratio of gonad mass to total body mass (gonadosomatic index, or GSI) because brook trout exhibit no post-fertilization parental care (Power 1980). Use of GSI as an index of reproductive effort can be problematic if individuals differ in their ability to acquire and utilize food resources. Consequently, I used the survival cost of reproduction as an indirect measure of effort. This cost is equal to the proportional reduction in overwinter survival of post-reproductive individuals relative to that of non-reproductive individuals of the same size and age.

My second objective was to assess the adaptive significance of life history variation within and among brook trout populations on a small geographical scale. I compared the fitness, r , associated with observed age-specific rates of survival and fecundity with the fitness values generated by potentially alternative age-specific schedules of fecundity and survival within and among populations. I assumed that an adaptive life history was one whose age-specific rates of survival and fecundity maximized r .

A major assumption of the analysis is that additive genetic variation exists for brook trout life history traits in the Cape Race (Newfoundland) populations. Indirect evidence suggests that this assumption is reasonable. Physical barriers prevent gene flow among populations, and geological evidence indicates that the populations have been isolated from one another since the Wisconsin glaciation (Rogerson 1981). The populations are electrophoretically distinguishable at several loci, with some enzymes being fixed for alternative alleles at the population level (Ferguson et al. 1991). Although the heritabilities of developmental and life history traits have not been measured for brook trout on Cape Race, several quantitative genetic studies indicate that significant additive genetic variation exists for such traits in salmonid fish (e.g., Gjedrem 1983, Thorpe et al. 1983, Gjerde 1984, 1986, Robison and Luempert 1984).

TABLE 1. Age-specific lengths observed for immature brook trout (both sexes) in southeastern Newfoundland June 1988 and estimated from regression equations for immature individuals during the reproductive period.*

Population	Observed		Expected		Annual proportional length increase
	Age (yr)	Length† (mm)	Age (yr)	Length (mm)	
Freshwater River	1	55.2 ± 4.3 (n = 277)			
	1.67	62.6 ± 6.3 (n = 157)	2	80.4	1.46
	2.67	83.4 ± 4.3 (n = 74)	3	97.4	1.21
	3.67	96.2 ± 5.4 (n = 57)	4	114.3	1.17
	4.67	110.7 ± 8.2 (n = 9)	5	131.3	1.15
Cripple Cove River	1	58.6 ± 7.3 (n = 277)			
	1.67	74.3 ± 8.3 (n = 155)	2	108.2	1.85
	2.67	112.4 ± 11.2 (n = 76)	3	140.7	1.30
	3.67	139.2 ± 7.6 (n = 28)	4	173.3	1.23
	4.67	165.5 ± 6.3 (n = 10)	5	205.8	1.19
Watern Cove River	1	60.2 ± 5.5 (n = 289)			
	1.67	74.8 ± 7.6 (n = 179)	2	104.2	1.73
	2.67	107.2 ± 8.4 (n = 117)	3	130.7	1.25
	3.67	129.8 ± 7.1 (n = 78)	4	157.2	1.21
	4.67	149.1 ± 5.7 (n = 17)	5	184.7	1.17

* Length (y) at age (x) regressions were: Freshwater River: $y = 16.98x + 46.42$ ($r = 0.93$); Cripple Cove River: $y = 32.55x + 43.07$ ($r = 0.95$); Watern Cove River: $y = 26.49x + 51.21$ ($r = 0.94$).

† Means ± 1 SD.

STUDY POPULATIONS

Brook trout life histories differ significantly among several populations on Cape Race, southeastern Newfoundland, Canada (bounded by 53°16' W, 46°45' N, 53°04' E, and 46°38' S; Hutchings 1990). The populations are unexploited, do not differ significantly in fish density, and do not experience interspecific predation or competition. With the exception of a small population of threespine sticklebacks, *Gasterosteus aculeatus*, in Cripple Cove River, brook trout are the only fish in these rivers (as determined by electrofishing over 4 yr), and potential avian predators do not inhabit Cape Race. Comparing the most divergent populations in terms of life history, females in Freshwater River reproduce at a 39% smaller size than those in Cripple Cove River but allocate 55% more body tissue to gonads. Larger eggs and higher fecundity at small body size contribute to the higher gonadosomatic index (GSI) in Freshwater females. The life history of trout in Watern Cove River is intermediate to those in the other two rivers.

Physically, these short (3–5 km axial length) and narrow (1–5 m) rivers differ primarily in the relative proportion of flat (slow-moving water, i.e., <40 cm/s)

and riffle (≥ 40 cm/s) habitat. River differences in the frequency of occurrence and total area of flat habitat have two main effects on brook trout life history (Hutchings 1990). First, the biomass of aquatic invertebrates—the main source of food for trout (Power 1980)—is almost three times higher in Cripple Cove than it is in Freshwater, resulting in significantly faster growth rates for Cripple Cove trout. Second, river differences in the relative abundance of deep (>40 cm) water appear to provide qualitatively different overwinter habitat among populations, leading to population differences in overwinter survival.

CALCULATION OF REASONABLE ALTERNATIVE LIFE HISTORIES

Fitness calculations

The fitness, r , of a phenotype p having a given lifetime age-specific schedule of fecundity and survival in environment (river) i is given by

$$1 = \sum l_x(p_i)m_x(p_i)e^{-rx}. \quad (5)$$

Although the use of r implies that selection on the traits of interest is density-independent, Sibly and Calow (1983:545–546), following Charlesworth (1980:172–

TABLE 2. Equations used in calculating alternative Newfoundland brook trout life histories. Units of measure: GSI (gonadosomatic index) = gonad mass divided by total body mass; length in millimetres; egg size (diameter) in millimetres. *P*-value of all regressions was <.05.

Freshwater River	
GSI = 0.0006(Length) + 0.1020	(<i>n</i> = 111; <i>r</i> = 0.33)
Fecundity = 1.18(Length) - 74.26	(<i>n</i> = 127; <i>r</i> = 0.81)
Egg size = 0.012(Length) + 3.203	(<i>n</i> = 114; <i>r</i> = 0.57)
Cripple Cove River	
GSI = 0.0006(Length) + 0.0248	(<i>n</i> = 48; <i>r</i> = 0.41)
Fecundity = 0.747($e^{0.031(\text{Length})}$)	(<i>n</i> = 65; <i>r</i> = 0.84)
Egg size = 0.007(Length) + 2.962	(<i>n</i> = 48; <i>r</i> = 0.39)
Water Cove River	
GSI = 0.0006(Length) + 0.0467	(<i>n</i> = 52; <i>r</i> = 0.39)
Fecundity = 1.30(Length) - 100.14	(<i>n</i> = 52; <i>r</i> = 0.64)
Egg size = 0.018(Length) + 1.880	(<i>n</i> = 52; <i>r</i> = 0.77)

173), have shown that fitness can be defined as *r* for populations subjected to either density-dependent or density-independent population regulation. Prout (1980) has also shown that selection on genotypes can be density independent within populations regulated by density. Maximizing *r* in a density-dependent population is equivalent to maximizing the number of individuals in the critical age group (Charlesworth 1980: 200).

Size of mature and immature females at age x

As with many organisms having indeterminate growth, age-specific rates in fish are best expressed in terms of body size, a character that is correlated with most life history traits in salmonid fish (Hutchings and Morris 1985). Size at the beginning of each annual reproductive period (the first 2–3 wk of October on Cape Race) is dependent on the state of maturity because maturation (production of competent gametes) reduces growth rate in salmonids (cf. Bell 1980, Jonsen 1985, Myers et al. 1986, Rowe and Thorpe 1990, Berglund et al. 1992).

To determine age-specific lengths of virgin females, and to incorporate the natural variability in size at age in each population, age-specific sizes were derived from the mean length at the end of the first year of life for each population. (Age was calculated from time of egg fertilization, i.e., October, so that integer values of age represent ages at the beginning of the reproductive period.) Beyond age 1 yr, females were assumed to grow at a rate that approximated the growth rate of non-maturing fish in each population. The latter growth rates were calculated from linear regressions that related length to age for immature fish aged 1.67 to 4.67 yr sampled in June 1988. (The qualitative results that emerged from this conservative estimate of growth rate were the same as those based on a method that gave maximal rates of growth.) Expected age-specific lengths of immature females during the reproductive period and expected age-specific growth rates (defined as proportional increases in length from year *x* to *x* + 1) are given in Table 1.

During the year of initial maturation, and for each year thereafter, annual growth rates were reduced to reflect the energy demands that gonadal production places on somatic growth. I assumed that the proportion of surplus energy allocated to gonads was directly related to the proportional loss of surplus energy devoted to somatic growth (Ware 1980, Sibly et al. 1985). Thus, I assumed that the annual growth rate of a fish that would reproduce at age *x* was reduced by an amount $(1 - \text{GSI}_x)^\beta$ such that

$$L_{Mx} = L_{Ix}(1 - \text{GSI}_x)^\beta. \quad (6)$$

To determine the age-specific lengths of reproductive females from the lengths they would have been had they not matured (i.e., determining L_{Mx} from L_{Ix}) and to incorporate size-dependent effects on GSI (cf. Table 2), I used the general form of the linear regression between GSI and body length (*L*), $\text{GSI} = \theta L_M + \epsilon$, where θ and ϵ are the slope and intercept, respectively. The lengths of mature females, L_M , can be calculated from the lengths they would have been had they not matured, L_I , from

$$L_M = L_I[1 - (\theta L_M + \epsilon)]^\beta. \quad (7)$$

For the age classes encompassing each population mean age at reproduction, the sums of squared deviations between observed and expected female lengths was minimized when $\beta = 1$. Thus, Eq. 7 simplifies to

$$L_M = L_I(1 - \epsilon)/(1 + \theta L_I). \quad (8)$$

Age-specific lengths of mature and immature females are presented in Table 3.

Age-specific survival

Field data were used to determine age-specific rates of survival. The survival data used here reflect the observation that 80–100% of the annual mortality in brook trout on Cape Race occurs during winter (Hutchings 1990). In the absence of size-specific survival data from the summer (May–September), summer survival probabilities were assumed to be equal to the estimated summer survival rates for age = 1.67 yr fish (0.85, 0.81

TABLE 3. Estimated age-specific lengths for virgin and reproductive female brook trout from three Newfoundland populations.

Population	Age at first reproduction, α (yr)	Lengths of virgin females (mm)	Age of female (yr)					
			2	3	4	5	6	7
			Lengths of females initially reproducing at age α (mm)					
Freshwater River	2	80.4	68.6	70.7	70.7	70.7
	3	97.4		82.4	82.4	82.4
	4	114.3			96.0	96.0
	5	131.3				109.0
Cripple Cove River	2	108.2	99.1	116.6	128.9	136.7	144.3	151.5
	3	140.7		126.5	139.3	146.7	154.5	161.2
	4	173.3			153.1	159.7	166.0	171.7
	5	205.8				178.7	183.2	192.6
Watern Cove River	2	104.2	93.5	104.5	111.4	115.1	118.9	...
	3	130.7		115.5	123.9	133.0	142.7	...
	4	157.2			136.9	138.7	140.5	...
	5	184.7				157.7	158.1	...

and 0.89 in the Freshwater, Cripple Cove, and Watern Cove rivers, respectively). For non-reproductive females, overwinter (October–April) survival equalled the population mean values of 0.31, 0.58, and 0.58 for Freshwater, Cripple Cove, and Watern Cove, respectively.

On average, reproduction reduces overwinter survival in female Cape Race brook trout by 58% (Freshwater River), 31% (Cripple Cove River), and 38% (Watern Cove River). These survival costs were determined from mark–recapture experiments of reproductive and non-reproductive individuals of the same size and age (described in J. A. Hutchings, *unpublished manuscript*). The possibility that the cost estimates were confounded by individual differences in quality (cf. Reznick 1985, Partridge 1989) is low. Survival prospects throughout life for Cape Race trout are highly dependent upon body size at the onset of each winter, probably through the positive influence of size on body fat (Brett et al. 1969, Elliott 1976). Experimental studies have demonstrated that for salmonid fish reproducing at the sizes of the Cape Race trout, initial differences in body size, or “quality,” between maturing (larger) and non-maturing fish of equal age at the onset of maturation usually disappear at the time of reproduction (e.g., Rowe and Thorpe 1990, Berglund et al. 1992). Even if size differences persisted, resulting in negatively biased cost estimates, costs underestimated by as much as 33% within each population do not affect the qualitative results presented here.

Post-reproductive survival is also strongly dependent on body size. Size-specific overwinter survival of post-reproductive females was calculated from empirically based normal probability density functions. These functions were those that minimized the sums of squares of the differences between observed and expected data. (The survival data are based on mark–recapture experiments conducted in Freshwater, Cripple Cove, and

Watern Cove rivers in 1988–1989 [J. A. Hutchings, *unpublished manuscript*].) The functions relating post-reproductive, overwinter survival (Y) to female body length (X , in millimetres) are:

$$\text{Freshwater: } Y = \frac{0.45}{\sqrt{\pi}} (e^{-0.5[(X-98.6)/9.4]^2}) \quad (9)$$

$$\text{Cripple Cove: } Y = \frac{1.17}{\sqrt{\pi}} (e^{-0.5[(X-154.0)/11.4]^2}) \quad (10)$$

$$\text{Watern Cove: } Y = \frac{0.91}{\sqrt{\pi}} (e^{-0.5[(X-129.1)/14.0]^2}) \quad (11)$$

Survival probabilities from birth to the end of the second winter (i.e., age = 1.67 yr) were calculated for each population by assuming that females reproducing at the modal age replaced themselves at equilibrium (i.e., age-specific summer and overwinter survival rates were constrained such that each female produced two offspring that survived to reproduce).

Age-specific fecundity

Age-specific rates of fecundity were calculated from empirical regressions that related number of eggs per female to body length (Table 2). The linear regression for Cripple Cove River could not be used because the length at the x intercept exceeded the lengths of some of the predicted age-specific lengths at reproduction. Thus a power function was used to describe fecundity as a function of female length (Table 2). The parameters of the function were based on the assumption that the minimum length at which a female could produce a single egg was 62.9 mm (the x intercept of the fecundity–length regression for Freshwater River females, the smallest reproductive females recorded for this species [Hutchings 1990]). The function presented in Table 2 minimized the sum of the squared deviations

between the observed and predicted size-specific fecundities for Cripple Cove River females.

For organisms in which offspring size varies with body size, age-specific fecundities should incorporate differential survival among offspring of different sizes. Egg diameter (E) was positively correlated with maternal body size among brook trout on Cape Race (Table 2). In the laboratory, post-hatching survival probability of brook trout (S) is positively correlated with egg volume ($V = \pi E^3/6$, in cubic millimetres) under non-ad libitum food conditions (Hutchings 1991), according to the equation $S = 0.013V + 0.026$ ($n = 11$ broods of 20 juveniles each; $r = 0.88$). Thus, age-specific fecundities were multiplied by the expected post-hatching survival probability of each age-specific egg size.

Juvenile and adult rates of survival and growth

To test the predictions of life history theory, it was necessary to calculate juvenile and adult values of survival and growth rate. For the survival calculations, the juvenile stage extended from birth until the optimal age at first reproduction and the adult stage extended from the latter age until death. To account for population differences in the lengths of the juvenile and adult periods, mean annual survival probabilities, weighted by the probabilities of attaining each age, were used to calculate the ratios of adult-to-juvenile survival. Sizes at age were those calculated in Table 2. Age-specific survival was calculated as indicated previously. Survival costs of reproduction were excluded from the adult survival probability estimates by dividing the size-specific values of overwinter survival by the mean decrements in overwinter survival of reproductive females relative to non-reproductive individuals. Juvenile growth rate was estimated as the length of individuals at the end of their first year of feeding. Adult growth rate was estimated as the difference in the lengths of individuals at the end of their first and third years of feeding. This approximation of adult growth ensured that all fish were larger than their minimum recorded size of reproduction (72 mm; Hutchings 1990) and minimized the probability of including previously mature adults in the empirical length data.

A test for adaptive variation in life history

The adaptive significance of observed brook trout life histories was assessed by comparing observed trait values with those predicted to maximize fitness. A direct comparison of observed and predicted ages at first reproduction was not possible because evidence of prior maturity could not be determined from the body scales (as areas of calcium resorption) of brook trout on Cape Race. Observed modal age at reproduction was used as an index of age at first reproduction and compared with predicted ages at first reproduction. Observed mean age at reproduction was compared with predicted mean ages at reproduction. The latter was calculated to be

TABLE 4. Age-specific data used to calculate juvenile and adult survival for females in three brook trout populations in southeastern Newfoundland. Juvenile and adult stages are separated by horizontal lines.

Age (yr)	Season*	Freshwater River	Cripple Cove River	Watern Cove River
0-1.67	1S, 2W	0.19	0.05	0.05
1	S	0.85	0.81	0.89
2	W	0.31	0.58	0.58
2	S	0.85	0.81	0.89
3	W	0.07	0.58	0.52
3	S	0.85	0.81	0.89
4	W	0.07	0.95	0.77
4	S	0.85	0.81	0.89
5	W		0.84	0.80
5	S		0.81	0.89
6	W		0.55	
6	S		0.81	
Weighted mean annual juvenile survival		0.38	0.21	0.22
Weighted mean annual adult survival		0.06	0.67	0.57
Ratio of adult/juvenile survival		0.16	3.19	2.59

* S = summer months of May through September; W = winter months of October through April.

$$\frac{[(n_{\alpha})(\alpha) + (n_{\alpha}\delta_{\alpha})(\alpha + 1) + (n_{\alpha+1}\delta_{\alpha+1})(\alpha + 2) + \dots + (n_{T-1}\delta_{T-1})(T)]}{\sum_{\alpha} n_{\alpha}}, \quad (12)$$

where n_{α} is the number of reproductive females at age α , δ_{α} is the overwinter survival probability of reproductive females at age α , α is the optimal age at first reproduction, and T is the age of death. Values of T equalled the oldest ages observed in the wild ($T = 5, 6, \text{ and } 7$ for Freshwater, Watern Cove, and Cripple Cove rivers, respectively).

RESULTS

Does age at maturity increase and effort decrease with increased adult survival?

The ratio of adult-to-juvenile survival differed 20-fold among populations (Table 4). Relative to juvenile survival, adult survival was lowest for Freshwater River trout and highest for Cripple Cove River trout. Comparing the most divergent populations, Freshwater River females matured earlier than Cripple Cove River females and had the lower ratio of adult-to-juvenile survival (Fig. 2A). Reproductive effort (gonadosomatic index, GSI) was negatively associated with adult-to-juvenile survival among populations (Fig. 2B). The more appropriate measure of effort—the survival cost of reproduction—was also negatively associated with relative adult survival (Fig. 2C). Thus, the population with the highest adult survival, relative to that of juveniles, matured latest, allocated the least amount of

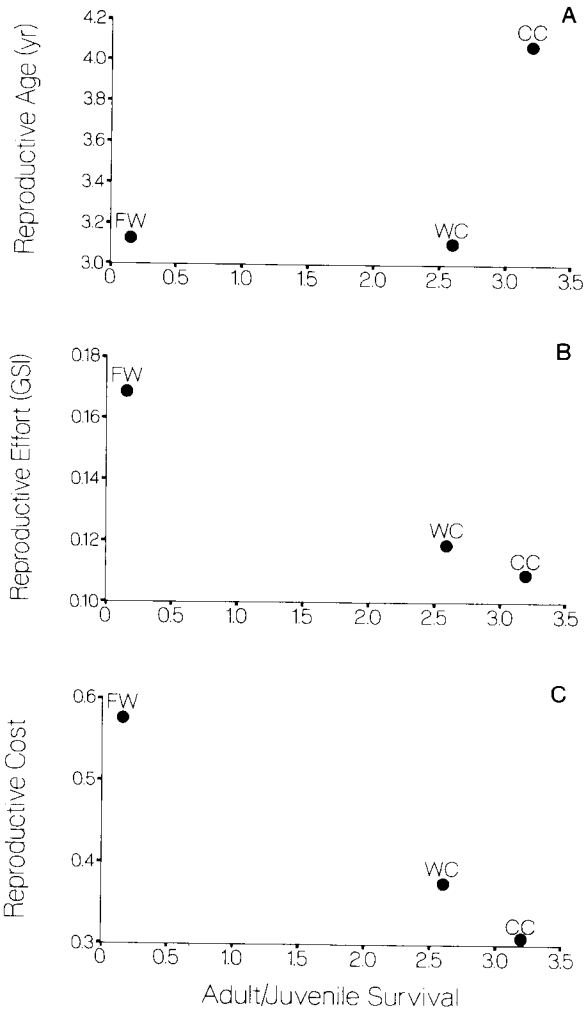


FIG. 2. Relationships between the ratio of adult to juvenile survival and (A) mean reproductive age, (B) reproductive effort (gonadosomatic index, GSI = gonad mass/total body mass), and (C) survival cost of reproduction ($1 - [\text{overwinter survival of reproductive fish}]/[\text{overwinter survival of non-reproductive fish}]$), controlled for fish size and age) in three southeastern Newfoundland populations of brook trout (*Salvelinus fontinalis*). Population abbreviations: CC = Cripple Cove River, FW = Freshwater River, WC = Watern Cove River.

body tissue towards reproduction, and experienced the lowest survival cost of reproduction.

Does age at maturity decrease and effort increase with increased juvenile growth?

The ratio of adult-to-juvenile growth rate differed 64% among populations, with Freshwater River and Cripple Cove River trout having the lowest and highest ratios, respectively. At the population level, age at reproduction was positively associated with adult-to-juvenile growth rate (data available for five Cape Race populations; Fig. 3A). Among Freshwater, Cripple Cove, and Watern Cove populations, individuals with the poorest prospects for growth as adults (i.e., Fresh-

water River trout) allocated the most body tissue to gonads (Fig. 3B) and experienced the greatest reproductive cost (Fig. 3C).

Are observed life histories adaptive?

A single optimum age at first reproduction was favored for female brook trout within each of the three populations (Fig. 4). Fitness was maximized for females reproducing initially at age 3 in Freshwater and Watern Cove rivers and at age 4 in Cripple Cove River. With one exception (Cripple Cove River), predicted ages at first reproduction equalled observed modal ages at reproduction (Fig. 5). Differences between predicted and observed mean ages at reproduction were small, ranging from 6% (Watern Cove River) to 8% (Cripple

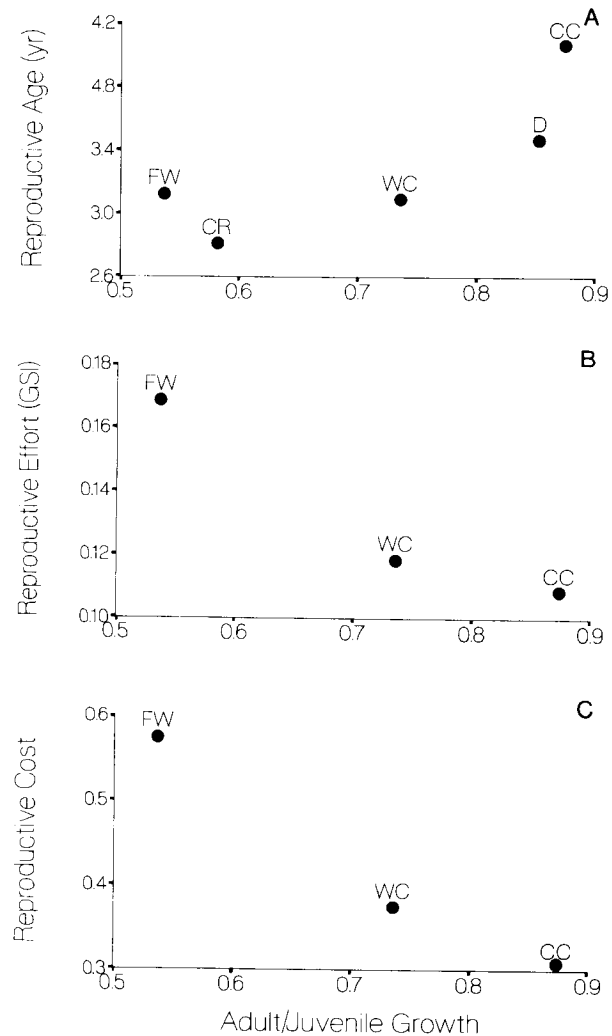


FIG. 3. Relationships between the ratio of adult-to-juvenile growth and (A) mean reproductive age, (B) reproductive effort (GSI), and (C) survival cost of reproduction (see Fig. 2 legend for definitions) in several Cape Race brook trout populations. Population abbreviations: CC = Cripple Cove River, CR = Cape Race River, D = Drook River, FW = Freshwater River, WC = Watern Cove River.

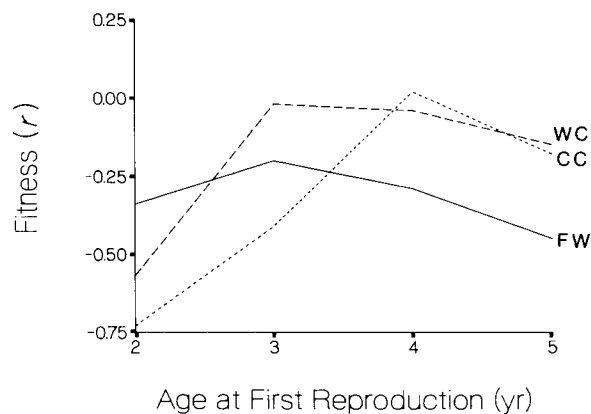


FIG. 4. Fitness (r) associated with four ages at first reproduction for females in three brook trout (*Salvelinus fontinalis*) populations in southeastern Newfoundland (FW = Freshwater River, CC = Cripple Cove River, WC = Watern Cove River).

Cove River). Overall, differences between observed and predicted data were significantly smaller than expected by chance ($P = .018$, based upon 1000 data randomizations). Within populations, females reproducing at an age earlier than the optimum were larger than predicted for that age (Table 5). The fitness of these fast-growing, early reproducing individuals exceeded that of individuals reproducing initially at the optimum age in two of the three populations.

DISCUSSION

Life history theory can account for population differences in reproductive age, size, and effort among Cape Race brook trout. Theory can also explain how changes in adult survival and growth rate, relative to juveniles, influence reproductive strategies within this species. Although the number of populations in the study was small, the probability of obtaining the associations predicted by theory for all six independent comparisons (Figs. 2 and 3) was significantly less than expected by chance ($P = .5^6 = .016$). Independently derived estimates of reproductive costs indicate that, irrespective of the cause(s), early reproduction coupled with high effort is associated with a high survival cost of reproduction in brook trout. The fitness functions derived here support the hypothesis that life history variation among brook trout populations on Cape Race

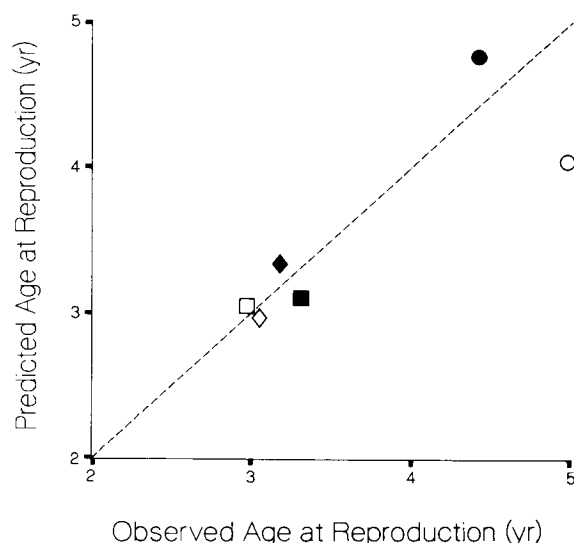


FIG. 5. Predicted and observed female reproductive age in three brook trout populations in southeastern Newfoundland. Solid symbols represent predicted vs. observed mean reproductive age; open symbols represent predicted age at first reproduction vs. observed modal age at reproduction (Freshwater River: ■, □; Cripple Cove River: ●, ○; Watern Cove River: ◆, ◇). Dashed line is the 1:1 reference of equality.

is adaptive. Compared with potentially alternative strategies, observed reproductive ages and age-specific rates of fecundity are those which maximize individual fitness.

Population differences in life history can be explained as adaptive responses to the ratios of adult-to-juvenile growth rate and survival. Reduced adult growth rate influences fitness in several ways. With respect to survival, it increases the time spent at a small size, during which trout are highly susceptible to overwinter mortality (cf. equations (9)–(11); J. A. Hutchings, *unpublished manuscript*). This is because small individuals utilize their proportionately lower lipid stores (Brett et al. 1969, Elliott 1976) at a faster rate than large individuals (Schmidt-Nielsen 1984) during the energetically demanding winter (Cunjak 1988). Thus, compared to Cripple Cove River trout, early reproduction is favored among Freshwater River trout because of the increased cost of mortality between successive reproductive ages that delaying reproduction would entail. The high probability of post-reproductive death

TABLE 5. Observed and predicted length at first reproduction and associated fitness (r) for females reproducing earlier than the optimal age at first reproduction in three populations of brook trout in southeastern Newfoundland.

Population	Age (yr)	Observed length (mm)	r	Predicted length (mm)	r	r at optimal age
Freshwater River	2	81.1	0.31	68.6	-0.34	-0.20
Cripple Cove River	2	119.0	-0.25	99.1	-0.73	0.02
	3	128.5	-0.34	126.5	-0.41	0.02
Watern Cove River	2	109.8	0.08	93.5	-0.57	-0.02

among Freshwater River females also favors high reproductive effort (Gadgil and Bossert 1970, Schaffer 1974). With respect to fecundity, slow growth reduces the rate at which fecundity increases with age, thus minimizing the importance of a primary factor favoring delayed reproduction (Schaffer 1979). Increased juvenile growth favors early reproduction because the main benefit of minimizing age at maturity, i.e., short generation time, is coupled with increased age-specific fecundity. Sufficiently low adult growth rates should also favor increased reproductive effort because, by defining fitness as r , a decline in the rate at which fecundity increases with age is analogous to an increase in the rate at which mortality increases with age. Low food abundance provides an additional selective factor favoring increased allocation of body tissue to gonads by selecting for larger offspring (Hutchings 1991).

The results are consistent with the hypothesis that brook trout life histories have evolved in response to selection acting on age- and size-specific rates of survival and fecundity. I have argued that population differences in these age-specific parameters have been effected by population differences in individual growth. Two alternative explanations are that brook trout life histories have evolved in response to population differences in density (MacArthur and Wilson 1967) or to environmental variation (Murphy 1968).

The observed life histories are inconsistent with the predictions of the density-dependence and environmental variability hypotheses. The density-dependence hypothesis predicts that, at high density, selection favors genotypes that delay reproduction and reduce effort (Pianka 1970). Among Freshwater, Cripple Cove, and Watern Cove rivers, population densities of 0.85 ± 0.30 , 0.79 ± 0.26 , and 1.09 ± 0.38 fish/m² (means ± 1 SD), respectively, do not differ significantly (densities based on the enumeration of all fish collected by electrofishing within enclosed 15–74 m² stations, six replicates per river; $F = 1.42$, $P = .33$, as determined by 1000 data randomizations). The population with the highest density (Watern Cove River) neither reproduced latest in life nor expended the lowest effort. Given the significantly low amount of food in Freshwater River, it could be argued that intraspecific competition—a correlate of density—was highest in Freshwater River. If this is true, the results remain inconsistent with the density-dependence hypothesis because Freshwater River females reproduced earliest and expended the greatest effort.

The environmental variability hypothesis predicts that individuals within populations experiencing repeated, unpredictable environmental fluctuations are favored to delay reproduction and, through reduced effort, to produce several broods throughout their lives (i.e., bet-hedging strategy; cf. Stearns 1976). Given their proximity to one another (1–4 km), the rivers are exposed to the same macro-climatic environment. Although time-series data on water temperature and ve-

locity for each river are not available, it is reasonable to expect the narrowest and shallowest river to be most sensitive to macro-climatic changes. Comparing the most divergent populations of Cripple Cove and Freshwater rivers, the latter is slightly shallower (16.8 ± 7.3 cm vs. 17.1 ± 8.8 cm; $P > .05$) and significantly narrower (3.4 ± 2.0 m vs. 4.8 ± 2.0 m; $P < .01$) than the former (means ± 1 SD). According to the environmental variability hypothesis, Freshwater River individuals should reproduce late and expend low effort whereas Cripple Cove River individuals should reproduce early and expend high effort—opposite to the observed data. Thus, population differences in brook trout life history on Cape Race appear not to be effected either by density or by fluctuations in the local environment.

The study provides theoretical and empirical support for the hypothesis that increased juvenile growth rate favors early reproduction within populations. A negative association between reproductive age and growth rate has been documented in fish (Alm 1959, Beverton and Holt 1959, Thorpe 1986) and in many invertebrates (e.g., *Drosophila melanogaster* [Robertson 1963]; amphipods [Doyle and Myers 1982], copepods [McLaren 1974, Myers and Runge 1983]), although, for invertebrates, this relationship can often be attributed to the reduced time at which a size or development threshold for maturity is attained. For fishes the relationship is governed largely by the links that exist between growth rate, fecundity, and survival (Beverton and Holt 1959, Gadgil and Bossert 1970, Pauly 1980, Roff 1984, present study). In a study of reaction norms for age and size at maturity (a reaction norm represents the range of phenotypes expressed by a genotype across an environmental gradient), Stearns and Koella (1986) concluded that within populations a decreased growth rate should always be accompanied by delayed maturity, although they did not differentiate adult from juvenile growth rate.

Reports of early reproduction being associated with slow growth rate have been cited as exceptions to the general trend, although these apparent incongruencies can be explained by life history theory. Leggett and Power (1969) compared two Newfoundland populations of ouananiche (freshwater Atlantic salmon, *Salmo salar*) and found that the population with delayed maturity also had the higher individual growth rate. But given that both populations had similar juvenile growth rates (Leggett and Power 1969), the observed association between growth rate and age at maturity is that which would be predicted by theory. Pinhorn (1969) compared two populations of Atlantic cod, *Gadus morhua*, and found that the slower-growing population matured at an earlier age. However, the slow-growing, early maturing population also had higher adult mortality (Pinhorn 1969), as predicted by life history theory. Alm's (1959) review reported that age at maturity is often higher in larger, fast-growing species or pop-

ulations. However, these patterns are not exceptions, because the level of comparison was among populations or among different species rather than among individuals within a single population. The present study suggests that valid comparisons among species or populations must include information on age-specific rates of survival and on both juvenile and adult growth.

Data presented here support the predictions that, relative to juveniles, low adult survival and growth rate favor high effort at an early age of reproduction. Although several studies from natural populations have been cited as supporting life history theory (e.g., Schaffer and Elson 1975, Leggett and Carscadden 1978, Stearns 1983), few include age-specific survival data on adults, and none express adult survival relative to juvenile survival (but see Morris 1992). The latter data are difficult to obtain because they require that the effects of reproduction be excluded from the adult survival probabilities. Nonetheless, studies for which survival data are available generally support the life history prediction regarding survival. Tinkle and Ballinger (1972) compared life history variation among lizard (*Sceloporous undulatus*) populations in the United States and found early age at reproduction associated with high adult mortality. Reznick et al. (1990) used a field-introduction experiment to demonstrate that guppies (*Poecilia reticulata*) responded to increased adult predation by maturing earlier in life and by increasing reproductive allotment (gonadosomatic index, GSI). Fox and Keast (1991) compared the life histories of pumpkinseed sunfish (*Lepomis gibbosus*) inhabiting environments that subjected populations to either low or high overwinter mortality. Populations that experienced high overwinter mortality matured 1–2 yr earlier and allocated almost twice as much body tissue to gonads as compared with fish in the low-mortality environment. Interestingly, Morris (1992) found that litter sizes (a measure of effort) in white-footed mice (*Peromyscus leucopus*) were not associated with adult-to-juvenile survival ratios as predicted by theory. He attributed the lack of demographic influence on litter size to the primacy of the effects of density and habitat selection. Schaffer and Elson (1975) provided the only test of the prediction that high adult growth rate should favor delayed reproduction (although they did not express adult growth relative to that of juveniles). They found that age at maturity in anadromous (seaward-migrating) Atlantic salmon increased with growth rate at sea. However, when errors in the data were corrected, the purported correlation was not significantly different from zero (Myers and Hutchings 1987).

It could be argued that the life history prediction based on adult and juvenile growth rates is a trivial consequence of growth rate being positively associated with survival. Although I used such an association to derive the prediction in Eq. 4, it is not a necessary

condition for the prediction to be true. Anadromous salmonid fish provide an excellent example of how the selective benefits of high age-specific fecundity can overcome the selective disadvantages of high, adult, age-specific mortality (cf. Gross 1987, Roff 1988). Relative to fresh water, the marine environment provides a rich food source for salmonids and allows for rapid growth with concomitant high age-specific fecundity, despite the significantly higher mortality experienced at sea. The fitness advantages of increasing age-specific fecundity in a high-mortality environment are great enough in some salmonids that anadromy has become a fixed trait (e.g., several species of Pacific salmon, *Oncorhynchus* spp.).

The present study provides direct field evidence of the importance of growth rate in life history evolution in fish. It demonstrates how growth-induced differences in age-specific survival and age-specific fecundity can shape patterns of covariation between age at maturity and reproductive effort. At the population level, relative rates of adult and juvenile growth can influence selection on mean age at maturity, while adaptive variation within populations can be the result of phenotypic plasticity. The influence of growth rate on life history evolution among populations and on individual optimization within populations merits further study. More generally, the conclusion that populations can be adapted to their local environment on a very small geographical scale raises serious questions concerning the utility of large-scale (e.g., latitudinal or inter-specific) comparisons as confirmatory (hypothesis-testing) rather than exploratory (hypothesis-formulating) analyses of life history theory.

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