BEHAVIOURAL IMPLICATIONS OF INTRASPECIFIC LIFE HISTORY VARIATION

JEFFREY A. HUTCHINGS

Institute of Cell, Animal and Population Biology, University of Edinburgh, West Mains Road, Edinburgh EH9 3JT, Scotland, UK

INTRODUCTION

In relative terms, life history theory predicts the age at which an organism should reproduce and the effort that it should expend on reproduction at that age. Although behaviour is a constituent part of reproductive effort, life history theory provides no predictions about specific changes in behaviour that can be expected from specific changes in life history. How might evolutionary changes in life history bring about evolutionary changes in behaviour? Is the implicit assumption of life history theory that sufficient behavioural variability exists to effect changes in reproductive effort always a valid one? My objectives are to use empirical data on brook trout, Salvelinus fontinalis, and Atlantic salmon, Salmo salar, i) to test two predictions of life history theory, ii) to predict how evolutionary changes in life history can effect evolutionary changes in behaviour, and iii) to show how empirical tests of a theory in behavioural ecology can be compromised by excluding information on life history.

The relationship between life history and behaviour has been examined in fish although the intent of much of this work has been one of assessing how behaviour early in life influences some aspect of life history later in life. For example, Metcalfe et al. (1989) demonstrated that larger and behaviourally dominant juvenile Atlantic salmon generally migrate to sea, and possibly mature, earlier than smaller, subordinate individuals. Rather than ask how behaviour influences life history, I consider the changes in behaviour that might be expected to result from specific changes in life history. This approach shifts the emphasis from the behavioural aspects associated with foraging, territorial defence (as it relates to food acquisition), and predator avoidance to those associated with reproduction, e.g. selection of nest site, mate choice, and mate competition. Gross (1991) recently used such an approach to assess the conditional behavioural tactics employed by small, early-maturing (“jack”) and large, late-maturing (“hooknose”) coho salmon, Oncorhynchus kisutch, during breeding.

I consider the behavioural implications of intraspecific life history variation at the level of the population and at the level of the individual. At the population level, I use empirical data on unexploited brook trout populations to show how selection of nest site, selection of mates, and levels of intrasexual competition can be influenced by evolutionary changes in life history. Within populations, I examine two ways in which increased growth rate influences life history and behaviour. For female brook
trout, increased growth rate favours earlier reproduction and increased reproductive effort (Hutchings, in press a). For male Atlantic salmon, increased growth rate also favours early maturation—as mature male parr (Myers et al., 1986). It is commonly thought that alternative maturation strategies in male Atlantic salmon coexist in an evolutionarily stable state through frequency dependent selection (Myers, 1986). By incorporating a measure of behavioural (varying numbers of male parr and anadromous males per anadromous female) and life historical reality (varying age at maturity among parr and among anadromous males) into fitness calculations for the two strategies, I show that the evolutionary stability of alternative male maturation strategies in Atlantic salmon, and perhaps other fish as well, is much more complicated than is currently believed.

LIFE HISTORY THEORY

Life histories reflect the ways in which individuals vary their age-specific expenditures of reproductive effort in response to physiologically and environmentally-induced changes in age-specific mortality. Strictly speaking, life history traits include age-specific rates of mortality and fecundity although this definition is usually extended to include characteristics that directly influence these parameters, e.g. age and size at first reproduction, egg size and parity. Age-specific fecundity and survival differ from these other traits in one important respect. They are direct components of fitness in the sense that an increase in either of these values increases fitness whereas maximum values of the other traits can be associated with intermediate levels of fitness (Charlesworth, 1980).

Life history theory assumes that natural selection favours those genotypes whose age-specific schedules of survival and fecundity generate the highest per capita rate of increase relative to other genotypes in the population. That is, selection tends to maximize \( r \) (Fisher, 1930; Charlesworth, 1980)—the intrinsic rate of natural increase—as given by the Euler-Lotka equation

\[
1 = \sum l_x m_x e^{-rx}
\]

where \( l_x \) represents survival from birth to the beginning of the breeding season at age \( x \) and \( m_x \) is the number of female zygotes produced by an individual at age \( x \). The left hand side of the equation equals one because each female is assumed to reproduce itself at equilibrium.

Life history theory seeks to predict the age-specific reproductive pattern that will evolve in environments that have defined effects on age-specific schedules of mortality and fecundity. Consider the life-cycle of an annual breeder that starts breeding at age=1, where \( m \) offspring are produced at each breeding attempt, \( s_i \) is the survivorship from birth to breeding at age 1, and \( s_a \) represents adult survival between breeding events. Following Schaffer (1974) and Charlesworth (1980), the Euler-Lotka equation can be simplified to

\[
e^r = s_i m + s_a
\]

Re-arranging this equation yields
\[ s_a = e^r - s_j m \]

which expresses the central tenet of life history theory that future adult survival is negatively associated with present fecundity (Williams, 1966).

The combinations of adult survival and fecundity that an organism can potentially achieve is assumed to be limited and to be constrained to a set of evolutionary options (Levins, 1968; Partridge and Sibly, 1991). The optimal life history is that combination of adult survival and fecundity that maximizes \( e^r \). Graphically, these optimal rates correspond to the point in the options set through which the fitness contour, i.e. Equation (3), passes and at which fitness, \( e^r \), the y-intercept, is maximized. Given an options set whose boundary is concave with respect to the origin (Figure 1), as juvenile survival increases, holding adult survival constant, the slope of the fitness contour becomes increasingly negative, and selection favours increasing fecundity, or reproductive effort, with a concomitant reduction in adult survival. Similarly, decreased \( s_j \) favours reduced effort.

Figure 1  Options set for present fecundity, \( m \), with adult survival, \( s_a \), and adult growth rate, \( g_a \). Straight line fitness contours correspond to Equation (3) for the survival fitness function and to Equation (5) for the growth fitness function. The slope of the contour equals juvenile survival, \( s_j \), when the ordinate equals \( s_a \) and juvenile growth rate, \( g_j \), when the ordinate equals \( g_a \).
Relatively high adult mortality also selects for genes that increase reproduction earlier rather than later in life (Charlesworth, 1980). Thus, life history theory predicts that high juvenile survival, relative to adult survival, favours increased reproductive effort and decreased age at first reproduction (assuming that fecundity does not change with age).

Life history theory makes a second main prediction—one related to growth rate. In addition to the trade-off between current fecundity and future survival, Schaffer (1974) considered a trade-off between present fecundity and future growth. The importance of this trade-off to the life histories of organisms that continue to grow following maturation (e.g. many species of fish, reptiles, amphibians, and plants) lies in the positive associations (generated by correlations with body size) that generally exist between growth rate and both fecundity and survival (cf. Law, 1979; Bell, 1980; Roff, 1984; Stearns and Koella, 1986). Assuming equal constants of proportionality between growth rate and survival, Equation (2) becomes

$$e^r = g_jm + g_a$$

or

$$g_a = e^r - g_jm$$

where $g_a$ and $g_j$ represent adult and juvenile growth, respectively. Assume that the options set for combinations of present fecundity and post-reproductive or adult growth is that given in Figure 1. Rapid juvenile growth, relative to adult growth, favours increased effort, $m$, whereas low values of $g_j$ select for decreased effort. Increased juvenile growth rate also results in increased fecundity in early life and this favours earlier age at first reproduction (Charlesworth, 1980). Thus, the second main prediction of life history theory is that, relative to adult growth rate, increased juvenile growth rate favours increased effort at an earlier age at first reproduction (assuming constant age-specific rates of survival) (cf. Hutchings, in press a).

**INTRASPECIFIC VARIATION AMONG POPULATIONS**

**Life History Differences Among Populations of Brook Trout**

Empirical life history data were collected from several brook trout populations on Cape Race, Newfoundland, Canada, in 1987 and 1988 (see Hutchings, 1990 for sampling protocol and river descriptions). Cape Race is located on the southeastern tip of the Avalon Peninsula and is bounded by 53°16'W, 46°45'N, 53°04'E, and 46°38'S. Brook trout are the only salmonids and, with few exceptions, are the only fish in these rivers. This removes the potentially confounding influences of interspecific competition and predation (birds do not prey on these populations) on life history. The 10–30 metre cliffs at the river mouths prevent migration between rivers, precluding gene flow between populations. The populations are electrophoretically distinguishable (Ferguson et al., 1991) and have probably been isolated from one another since the Wisconsin glaciation, 10–12 000 years ago (cf. Rogerson, 1981).

In terms of life history, Cripple Cove (CC) and Freshwater (FW) are the most divergent populations on Cape Race. Relative to CC females, FW females matured, on average, at a 39% smaller size (99.8±17.8 mm fork length) but allocated 55% more body tissue to gonads. The ratio of gonad weight to total body weight,
expressed as the gonadosomatic index (GSI), was 0.17±0.03 and 0.11±0.02 for FW and CC females, respectively. In part, population differences in GSI were due to differences in size-specific fecundity—FW females produced more eggs per unit body mass than similarly sized CC females. However, most of the differences in GSI were due to differences in egg size. FW females produced 35% larger eggs (volume=46.5±12.1 mm³) than their CC counterparts.

**Fitness Calculations**

If brook trout life histories on Cape Race are adaptive, the observed patterns of age-specific survival and fecundity should generate the highest fitness relative to other potential age-specific combinations of survival and fecundity. To calculate fitness, \( r \), it is necessary to have reliable, empirically-based estimates of age-specific fecundity and survival as well as estimates of the degree to which these parameters are influenced by other traits, e.g. egg size, body size, and growth rate (see Hutchings, in press a, for details of these analyses).

Survival was calculated separately for the summer (May–September) and winter (October–April) months (details of the survival data are given in Hutchings, 1990 and Hutchings, unpublished data). Summer survival rates were determined from a static life table and were assumed to be independent of body size. (Violation of this assumption will have little effect on the analysis given that 70 to 80% of the annual mortality at the population level occurs during winter.) Mean overwinter survival ranged from 0.13 for FW females to 0.40 for CC females.

Overwinter survival generally increased with body size. This association probably has a physiological basis. Brook trout rely upon lipid reserves to survive the winter (Cunjak, 1988). Small individuals are disadvantaged primarily because, relative to large individuals, they utilize their proportionately smaller fat stores (Brett *et al.*, 1969; Elliott, 1976) at a faster rate (Schmidt-Nelson, 1984; Dunbrack and Ramsay, unpubl.).

The dependence on lipid reserves during winter is the basis for the primary cost of reproduction in brook trout on Cape Race. This survival cost, defined as the proportional reduction in overwinter survival of mature females relative to that of immature females of the same size and age, increases with effort (approximated as GSI) within and among populations and is dependent on body size—the smallest individuals experience disproportionately high costs relative to their effort (Hutchings, unpublished data).

To determine body sizes at different ages, I used empirical data for immature individuals (Hutchings, in press a). I assumed that maturation reduced growth rate during the year preceding reproduction by an amount equal to expected GSI, i.e. the proportion of surplus energy allocated to gonads was directly related to the proportional loss of surplus energy devoted to somatic growth. Survival in early life was directly related to the size of egg from which an individual was produced (Hutchings, 1991).

Age-specific fecundity rates were calculated from the empirical data on the Cape Race populations. Fecundity depended upon egg size and GSI, all three of which were positively associated with body size.
Variation in Age at Maturity

To determine whether the inter-population differences in age at maturity were adaptive, I calculated the fitness (r) associated with the observed age-specific schedules of fecundity and survival and compared this with the fitness of potentially alternative life histories within three populations (FW, CC, and Water Cove [WC]). The fitness calculations indicated that the optimal age at first reproduction (i.e. the age of initial maturity that maximized fitness) for females in FW, WC, and CC was 3, 3, and 4 years, respectively. These accord well with observed modal ages at maturity which were 3, 3, and 5 years for FW, WC, and CC, respectively (modal ages were used because ages at first reproduction, revealed as spawning checks in some species, cannot be discerned reliably from calcified structures in brook trout). I calculated predicted mean ages at maturity by assuming that individuals matured initially at the calculated optimal age and survived according to observed rates of age-specific survival. The differences between expected and observed ages at maturity were small, being 6% for WC, 7% for FW, and 8% for CC. The similarity between observed and predicted data support the hypothesis that population variation in age at maturity among Cape Race brook trout is adaptive (Hutchings, in press a).

Variation in Reproductive Effort (GSI)

To assess the degree to which observed levels of effort were optimal, I calculated fitness as a function of age at first reproduction for CC and FW populations at two levels of effort—0.11 and 0.17, the observed mean GSIs for CC and FW, respectively. (The fitness calculations controlled for the changes in post-reproductive survival effected by changes in GSI.)

The results support the hypothesis that observed levels of effort are adaptive. The fitness functions that incorporated the observed GSI values yielded the greater fitness for all potential ages at first reproduction (2–5 years). The fitness of FW females was greater (14–22%) at high effort whereas the fitness of CC females was greater (9–25%) at low effort.

Variation in Egg Size

The adaptive significance of inter-population variation in egg size can be assessed by considering the differences in food abundance among rivers. The biomass of aquatic stream invertebrates—the main source of food for brook trout (Power, 1980)—differed almost three-fold between CC and FW. The mean biomass of invertebrates per colonization bag in CC was 1.10 ± 0.59 g m⁻² as compared with 0.39 ± 0.15 g m⁻² in FW.

Smith and Fretwell (1974) and Kaplan and Cooper (1984) predicted that natural selection favours increased offspring size with reductions in food abundance. This prediction is based on the observation that 1) larger offspring are produced from larger eggs, and 2) competitive success for scarce resources is directly related to body size. Hutchings (1991) evaluated the fitness consequences for female brook trout of producing eggs of different sizes in environments having different amounts of food. Maternal fitness was optimized when females produced small numbers of large eggs under low food conditions and large numbers of small eggs under high
food conditions. Thus, the population differences in egg size among the Cape Race populations can be explained as adaptive responses to local differences in food abundance.

Tests of Life History Theory

To test the predictions of life history theory, it was necessary to calculate juvenile and adult values of survival and growth rate (details in Hutchings, in press a). For the survival calculations, I assumed that the juvenile stage extended from birth to the optimal age at first reproduction and that the adult stage extended from the optimal age at first reproduction to death. As I have estimates of the survival costs of reproduction for these populations (Hutchings, unpublished data), I used the survival probabilities of non-reproductive adults in these calculations. Because of population differences in ages at first reproduction and death, mean annual juvenile and adult survival probabilities were used in the analysis. 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 length of individuals between the end of their first year of feeding and the end of their third year of feeding. This approximation of adult growth rate ensured that all fish were larger than their physiologically minimum size of reproduction (Hutchings, 1990) and minimized the probability of including previously mature adults in the sample.

The ratios of juvenile to adult survival and of juvenile to adult growth differed dramatically among populations (Table 1). The empirical data support the predictions of life history theory. Relative to adults, both high juvenile survival and high juvenile growth rate were associated with early reproduction, high effort, and a high cost of reproduction.

Reznick et al. (1990) found that high adult mortality in guppies, *Poecilia reticulata*, favoured early reproduction and high effort. Their experiments were supported by a transplant experiment in the field and by laboratory work which indicated that the observed life histories had a genetic basis. Schaffer and Elson (1975) reported that high adult growth rate favoured delayed reproduction in Atlantic salmon although their data base was not a reliable one (Myers and Hutchings, 1987a).

<table>
<thead>
<tr>
<th>Population</th>
<th>Trait</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>$s_j/s_a$</td>
</tr>
<tr>
<td>Freshwater</td>
<td>6.25</td>
</tr>
<tr>
<td>Water Cove</td>
<td>0.39</td>
</tr>
<tr>
<td>Cripple Cove</td>
<td>0.31</td>
</tr>
</tbody>
</table>
Behavioural Implications of Adaptive Variation in Age at Maturity

Selection of mates

Evolutionary changes in age at maturity will affect concomitant changes in body size at maturity. Body size is an important determinant of breeding success in salmonids (e.g. van den Berghe and Gross, 1989), making it a likely candidate for sexual selection. For example, there is evidence that male sockeye salmon and kokanee, *O. nerka*, (Foote, 1988), coho salmon and threespine sticklebacks, *Gasterosteus aculeatus*, (Sargent et al., 1986) use body size as a proximate cue to assess the reproductive quality of potential mates. Selection favouring reduced age at maturity results in reduced mean size at maturity and reduced variation in size at maturity. Reduced variation in body size among spawning individuals should *ceteris paribus* reduce the scope for mate choice on the basis of body size.

One consequence of life history variation at the population level may be a shift from one potentially sexually selected trait to another (Partridge and Endler, 1987). Male brook trout compete with one another for access to a single female who selects the nest site and defends it against other females (see Power, 1980). Male trout take on an orange-red coloration during the autumn (Ricker, 1932). Although there are no empirical data on interpopulation variation in body coloration in brook trout (Power, 1980 does indicate that colour intensity may increase with body size), visual inspection of trout from Cape Race indicates that such variation exists (pers. obs.). One would predict that males in those populations for which early age at maturity is favoured should express greater intensities or amounts of the orange-red colour than populations for which delayed reproduction is favoured. This is because early-maturing males are less variable in body size and because their reproductive strategy is one that favours semelparity. Similarly, female preference for males in early-maturing populations would be predicted to be more dependent on body colour than in late-maturing populations. The existence of adaptive variation in male body coloration and genetic variation in female choice among guppy populations (Houde, 1988; Houde and Endler, 1990) suggests that life history evolution can effect similar variation among salmonid populations.

Selection of nest sites

Decreased size at maturity also has important consequences for selection of nest sites. Brook trout bury their eggs in the stream substrate but the size of substrate particle that females are able to displace is directly related to their body size (cf. van den Berghe and Gross, 1984). Thus, small females can only bury their eggs in substrate comprised of particles of small size. Such substrate is at a premium in short, northern boreal streams in which water velocities are generally high. Thus, reduced availability of suitable spawning sites may effect increased densities of spawning fish. This is indeed the case in Freshwater and Watern Cove populations for which early age at maturity is favoured. Most of the spawning in these rivers occurs in relatively calm channels separate from the main stem of the rivers. Spawning densities can reach 7.8 and 16.0 fish m\(^{-2}\) in WC and FW populations, respectively, and result in a high incidence of nest site superimposition (pers. obs.).

From a behavioural perspective, high-density spawning environments were forced upon these fish by life history pressures through selection for early age at maturity. Such a spawning environment, relative to that typically encountered by members of this species, must result in substantially different decision-making
processes and behavioural tactics with regard to selection of nest sites, selection of mates, and levels of aggression during mate competition.

INTRASPECIFIC VARIATION IN LIFE HISTORY WITHIN POPULATIONS

Adaptive Phenotypic Plasticity and Individual Optimization

The capacity of a genotype to alter its phenotype in response to environmental changes is termed phenotypic plasticity (Bradshaw, 1965). Plasticity can reflect either an environmentally-induced constraint on an individual's physiological state or it can represent an adaptive response to environmental change (e.g. varying population density, resource supply, temperature). Adaptive phenotypic plasticity can evolve as a norm of reaction, i.e. the systematic change with which a genotype alters its phenotypic expression across an environmental gradient (Schmalhausen, 1949; Stearns and Koella, 1986). Reaction norms have been shown to be heritable and to respond to selection (reviewed by Thompson, 1991).

One consequence of adaptive phenotypic plasticity is individual optimization of life history. For example, there is evidence that avian clutch size depends largely on individual ability to acquire food such that the clutches represent optimal responses by individuals to their local environment (reviewed by Lessells, 1991).

Adaptive phenotypic plasticity, or individual optimization, can be expected to evolve when (i) the spatial distribution of individuals across habitats is random with respect to genotype and when (ii) habitat significantly influences fitness. These conditions probably exist for many stream-dwelling salmonid fish. Following yolk sac resorption, juvenile brook trout emerge from the stream substrate in spring and are carried downstream to small, relatively discrete sections of slow-moving water where they spend most, occasionally all, of the summer months (Hutchings, 1990). The environment inhabited by these juveniles is probably random with respect to genotype because emerging individuals are unable to swim against all but the weakest of currents. And, as growth rate can vary significantly among individuals within and among juvenile habitats (Hutchings, unpubl. data), environmental variation can influence fitness through size-dependent effects on life history traits (Hutchings and Morris, 1985).

If body size influences the relationship between cost and effort, individuals may allocate their own optimal effort subject to their ability to survive reproduction and to their prospects for increasing fecundity in subsequent spawnings. To explore this possibility, I used empirical data from the Cape Race brook trout populations to construct age-specific reaction norms between reproductive effort at age of first reproduction and female body size. My approach was to calculate the fitness associated with different growth rates, different levels of effort, and different ages at first reproduction for each of the populations (details in Hutchings, in press b).

Reaction norms for body size and reproductive effort varied with age at first reproduction. The general pattern that emerged was that selection favoured maximal effort independent of body size when age at first reproduction was low (fastest growing females mature earliest) but favoured an increase in effort with size from minimal to sub-maximal effort when age at first reproduction was high (slowest growing females matured latest in life; Figure 2). Thus, when growth rates vary among individuals, selection should modify individual effort on a size-dependent basis according to the shape of the effort:size reaction norm.
Figure 2  Reaction norms for reproductive effort and body size for female brook trout in Cripple Cove River. Solid and dashed reaction norms refer to females maturing initially at ages 2 and 5, respectively.

Is there any evidence that individual fish optimize their effort in this manner? The reaction norms predict that females reproducing for the first time early in life should maximize effort. Thus, the GSI values for such fish should fall above the regression line relating GSI to body length. Although the data are few, they do support the prediction that the effort of FW females reproducing for the first time is greater than that which would have been predicted by body size alone (Figure 3).

Behavioural Implications of Intrapopulation Variation in Effort

Does a fish for which selection favours maximal effort behave differently from a fish for which selection favours a sub-maximal expenditure of effort? At the species level, semelparous salmonids defend their nest sites for more than a week following reproduction (van den Berghe and Gross, 1986) whereas iteroparous brook trout typically abandon their nests within hours after spawning (Power, 1980). Body coloration and aggression are much more intense among semelparous species of killifish than they are among iteroparous species (van Ramshorst and van den Nieuwenhuisen, 1978).

Maghnagen (1990) compared the nest-building behaviour of an iteroparous and a semelparous species of goby in the presence and absence of a predator. She found that the iteroparous goby significantly reduced the numbers of nests built in the presence of a predator whereas the nest-building behaviour of the semelparous goby was unaffected by the predator. Maghnagen (1990) also reported age-related, within-population variation in reproductive behaviour. For the iteroparous goby, older males built significantly more nests in the presence of the predator than younger
Figure 3  Gonadosomatic index (GSI=gonad weight/total body weight) as a function of body size for virgin female brook trout (age = 2yr) in Freshwater River (FW). Regression between GSI and length for all females in FW is indicated by the solid line.

males. This suggests that individuals are able to modify their reproductive behaviour in relation to their future expectation of producing offspring, i.e. their reproductive value (Fisher, 1930). Intuitively, it seems reasonable to expect adaptive plasticity in behaviour to co-evolve with adaptive plasticity in effort.

Alternative Mating Strategies

Phenotypically plastic spawning behaviour exists for many male salmonids. For one species, the iteroparous Atlantic salmon, males commonly mature as one of two life history forms (Jones, 1959). Parr mature in fresh water and are usually 2–4 years younger and 50–60 cm smaller than anadromous males which mature following a feeding migration to sea. Prior to spawning, a dominant anadromous male defends access to an anadromous female while mature male parr establish a linear dominance hierarchy immediately downstream of the courting pair with the largest parr usually nearest the female (Jones, 1959; Myers and Hutchings, 1987b). Mature male parr dart in close to the anadromous pair and shed sperm at the time of egg extrusion (Jones, 1959). Several males fertilize the eggs of a single female and males spawn with more than one female. The sex ratio of anadromous females to anadromous males usually exceeds unity. The ratio of mature male parr to anadromous males exceeds 20:1 at the spawning site in some populations (Hutchings, 1986). The incidence of parr maturation among male Atlantic salmon ranges from 1 to 100% in 28 Canadian populations (Myers et al., 1986).

Early maturity in male Atlantic salmon appears to be under both genetic and environmental control. Additive genetic variation (i.e. narrow-sense heritability;
Falconer, 1989) has been detected for parr maturation in hatchery environments (Naevdal et al., 1976). Thus, parr maturation appears to be a polygenic trait yet its expression is discrete—a male either matures as a parr or it does not. Myers and Hutchings (1986) modelled parr maturation as a threshold character having an underlying normal distribution for liability (Falconer, 1989). This implies that there is a genetically-determined threshold, perhaps in the levels of specific proteins, hormones or lipids (cf. Rowe et al., 1991), above which males mature as parr. For males whose genotype includes such a threshold, the expression of early maturity appears to depend on growth rate (Thorpe, 1986). Within and among Canadian populations, the covariation between growth rate and parr maturity produces a relationship characterized by a size or growth rate threshold below which males do not mature as parr (Myers et al., 1986). The logistic relationship between growth rate and parr maturity provides support for the genetic threshold hypothesis. The observation that the fastest-growing males mature earliest in life supports the individual optimization hypothesis and one of the predictions of life history theory.

Alternative male maturation strategies are thought to exist in evolutionarily stable proportions through frequency-dependent selection (Gross, 1985; Myers, 1986). The evolutionarily stable proportion of males in a population that mature as parr is that proportion which yields equal fitness for parr and anadromous males (Maynard Smith, 1982). Two implicit assumptions of this model for Atlantic salmon are that the fertilization success of parr is independent of the number of anadromous males present and that age at first reproduction among male parr does not vary within populations.

Using age-specific survival data for a Newfoundland population (Hutchings and Myers, 1986) and using egg fertilization rates calculated from the laboratory (Hutchings and Myers, 1988), I calculated the fitness, r, associated with adopting parr and anadromous male strategies under different densities of parr and anadromous males (details in Hutchings, unpublished data). I assumed here that total parr fertilization success would be reduced by a proportion equal to 1/n, where n was the number of anadromous males per female. Equilibrium parr densities were calculated to be the parr densities at which the fitness of individuals from the same cohort (i.e. born at the same time) adopting parr and anadromous male strategies were equal. That is, the “decision” either to reproduce during the autumn or to migrate to sea the following spring was made by all males at the same age such that parr matured initially at age x and anadromous males at x+2.

Parr and anadromous male behaviour, regarding mate choice and mate competition, depends on their respective densities. Equilibrium mature parr densities (an approximation of the proportion of males in a population maturing as parr) decline as the density of anadromous males increases (Figure 4). This is because the presence of a second, third, or fourth anadromous male probably displaces the hierarchical group of male parr further downstream, further away from the female, and reduces their chances of fertilizing eggs. From a behavioural perspective, parr mate choice decisions will not be clear-cut, such as “always choose the female with the fewest number of parr” or “always choose the female with the fewest number of anadromous males”, because parr fitness is conditional upon the numbers of both parr and anadromous males present during spawning.
Figure 4  Fitness functions for mature male parr (bold lines) and anadromous male Atlantic salmon (assumed to be of the same cohort) at spawning densities of 1 (—) and 4 (---) anadromous males per spawning female. The equilibrium parr densities at which the fitness of parr and anadromous males is equal are indicated by $d^*_1 = 7$ and $d^*_4 = 2.5$ parr per anadromous female.

From a life history perspective, variation in age at first reproduction among parr and anadromous males imposes additional complexity upon equilibrium proportions of parr and anadromous males within populations (Figure 5). The earlier reproduction occurs in life, the higher the fitness for both parr and anadromous males but, more importantly, equilibrium parr density increases as age at maturity decreases (ages refer here to age at first reproduction for parr and to age at seaward migration by anadromous males; males were assumed to spend one winter at sea). From an individual parr's perspective, his choice of female and his choice of the level of mate competition he is willing to engage will depend on his age. Evolutionarily, a male parr reproducing initially at a young age can tolerate a much larger group than parr mating initially at an older age because of the decline in equilibrium parr density with increased age at first reproduction.

There are no empirical data to test the predictions that parr reproductive success is influenced by the spawning density of anadromous males or that mate choice by parr is conditional in an age-specific manner. The potential for such individual optimization of behaviour and the implications it has for the stable coexistence of alternative mating strategies warrants experimental study.

SUMMARY

The behavioural implications of intraspecific life history variation are examined within and among populations. At the population level, brook trout life history variation appears to be adaptive and it supports the predictions of life history
theory that high reproductive effort and early reproduction are favoured by high juvenile:adult survival and by high juvenile:adult growth rate. Selection for reduced age at maturity can influence the selection of mates by changing the relative importance of traits under sexual selection and by affecting the selection criteria for choosing nest sites.

Within populations, variation in growth rate should result in individual optimization in life history and in the behavioural tactics associated with reproduction. There is some evidence that individual behaviour and reproductive effort is related to reproductive value. By incorporating realistic behavioural and life historical assumptions in fitness calculations for alternative maturation phenotypes in male Atlantic salmon, the evolutionary stability of alternative maturation phenotypes and the behavioural tactics adopted during spawning are shown to be considerably dynamic and complex phenomena.

ACKNOWLEDGMENTS

I gratefully acknowledge the financial support provided by a Postdoctoral Fellowship and a Postgraduate Scholarship from the Natural Sciences and Engineering Research Council (NSERC) of Canada, a NSERC Operating Grant to Douglas W. Morris, a Sigma Xi Grant-In-Aid of Research, an Atlantic Salmon Federation Olin Fellowship, and a Department of Supply and Services contract (Unsolicited Proposal UN-N-222). I have benefited from discussion with Joe
Brown, Doug Morris, Ram Myers and Linda Partridge and I am grateful to Neil Metcalfe, Linda Partridge and Gunilla Rosenqvist for comments on an earlier draft.

References


