The evolution of alternative mating strategies in variable environments

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Summary

We assessed the influence of phenotypic plasticity in age at maturity on the maintenance of alternative mating strategies in male Atlantic salmon, *Salmo salar*. We calculated the fitness, *r*, associated with the parr and the anadromous strategies, using age-specific survival data from the field and strategy-specific fertilization data from the laboratory. The fitness of each strategy depended largely on mate competition (numbers of parr per female, i.e. parr frequency) and on age at maturity. Fitness declined with increasing numbers of parr per female with equilibrium frequencies (at which the fitnesses of each strategy are equal) being within the range observed in the wild. Equilibrium parr frequencies declined with decreasing growth rate and increasing age at maturity. Within populations, the existence of multiple age-specific sets of fitness functions suggests that the fitnesses of alternative strategies are best represented as multidimensional surfaces. The points of intersection of these surfaces, whose boundaries encompass natural variation in age at maturity and mate competition, define an evolutionarily stable continuum (ESC) of strategy frequencies along which the fitnesses associated with each strategy are equal. We propose a simple model that incorporates polygenic thresholds of a largely environmentally-controlled trait (age at maturity) to provide a mechanism by which an ESC can be maintained within a population. An indirect test provides support for the prediction that growth-rate thresholds for parr maturation exist and are maintained by stabilizing selection. Evolutionarily stable continua, maintained by negative frequency-dependent selection on threshold traits, provide a theoretical basis for understanding how alternative life histories can evolve in variable environments.

Keywords: alternative mating strategies; environmental variability; life history evolution; salmonid fish; phenotypic plasticity

Introduction

The inability of genotypes to control the dispersal of their offspring among spatially heterogeneous environments should favour adaptive phenotypic plasticity in life history (Bradshaw, 1965; Levins, 1968; Houston and McNamara, 1992). When life history trait optima differ among environments that are inhabited largely at random within and among generations, selection acts on the way in which a genotype alters its life history traits in response to environmental change, i.e. selection acts on a trait's norm of reaction (Schmalhausen, 1949; Via and Lande, 1985; Gavrilets and Scheiner, 1993). One such reaction norm is a negative association between age at maturity and growth rate. For indeterminantly growing organisms, abundant evidence (Alm, 1959; references in Hutchings, 1993a) indicates that fast-growing individuals mature earlier than slow-growing individuals and empirically-based simulations suggest that such a norm of reaction is adaptive (Stearns and Koella, 1986; Kawecki and Stearns, 1993; Hutchings, 1993b).

Adaptive phenotypic plasticity appears to underlie a life history response by male Atlantic

salmon, *Salmo salar*, to changes in juvenile growth rate. Following a migration to sea as smolts, *anadromous males* return to their natal river and mature relatively late in life (age 4–7 years) at a large size (50–90 cm); *mature male parr* do not migrate to sea prior to reproduction and mature earlier in life (age 1–4 years) at a 70–90% smaller size (Jones, 1959; Thorpe, 1986). Field (Myers *et al.*, 1986) and laboratory data (summarized by Thorpe, 1986) indicate that males that mature as parr grow faster as juveniles in early life than do males that adopt the anadromous strategy. Prior to mating, parr establish a dominance hierarchy immediately downstream of a courting anadromous male and female and generally avoid detection by minimizing their movements while maintaining position on the stream substrate (Jones, 1959; Myers and Hutchings, 1987). When the female releases her eggs, parr 'sneak' under the female and shed sperm in competition with the anadromous male. Experimental work has shown that the fertilization success of anadromous males and mature male parr is negatively frequency-dependent (Hutchings and Myers, 1988) and that these alternative strategies have a heritable basis (Naevdal *et al.*, 1976; Thorpe, 1986).

Alternative mating strategies can be maintained within populations through negative frequency-dependent selection (Slatkin, 1978; Partridge, 1988). Such selection is presumed to maintain reproductive polymorphisms in salmonid fish (Gross, 1985, 1991a,b; Leonardsson and Lundberg, 1986; Myers, 1986). The frequencies of the strategies within populatations are evolutionarily stable when individuals adopting each strategy have equal fitness and when such populations cannot be invaded by individuals adopting other strategies (Maynard Smith, 1982; Parker, 1984). Thus, it is assumed that there exists a fitness function for each strategy, that the fitness of each strategy declines as the proportion of the population adopting that strategy increases and that the equilibrium frequencies of the two strategies occur at the point of intersection of the two functions.

A critical assumption of this model is that age at maturity is invariant within strategies. This assumption is clearly invalid in organisms for which age at maturity and its concomitant effects on fitness is influenced strongly by unpredictable variation in growth rate. In salmonids, growth rate varies significantly among juveniles of the same age (e.g. Metcalfe *et al.*, 1992) and this variation seems predominantly to be a function of the environment. Upon emergence from gravel egg nests, most salmonids are transported downstream to small, relatively discrete sections of slow-moving water where they spend most of their first growing season (Northcote, 1984; J.A. Hutchings, submitted). Juveniles utilize these habitats largely at random with respect to genotype because of the inability of recently-emerged juveniles to swim against all but the weakest of water currents and because of significant discordance in emergence times among siblings coupled with temporal variation in stream hydrography (Field-Dodgson, 1988; Snucins *et al.*, 1992). Thus, it is unlikely that recently-emerged siblings will be distributed into the same habitat. Among brook trout, *Salvelinus fontinalis*, 2-fold differences in growth rate 10 weeks following the initiation of exogenous feeding can persist as 40% differences in growth rate to maturity (J.A. Hutchings, submitted). In addition to altering age at maturity, growth rate can effect changes in fitness through size-dependent effects on other life history traits (e.g. Hutchings and Morris, 1985; van den Berghe and Gross, 1989).

It is not clear, then, how alternative reproductive strategies can be evolutionarily stable within populations (1) that experience environmental heterogeneity largely at random with respect to genotype and (2) for which habitat quality significantly influences fitness. The primary objective of this paper is to assess the influence of phenotypic plasticity in age at maturity on the evolution and maintenance of alternative reproductive strategies in male Atlantic salmon. We used age-specific survival data largely from a single population in southwestern Newfoundland (Myers, 1984; Hutchings and Myers, 1986) and egg fertilization data on parr and anadromous males in the

Table 1. Survival estimates for immature and mature male Atlantic salmon in the Little Codroy
River, Newfoundland

Life stage	Age on October 1 (years)	Season	Immature males	Mature males
Parr	1	W S	0.27	0.27
	2	W	0.44	0.44
		S	0.75	0.75
	3	W	0.55	0.40
		S	0.80	0.59
	4–6	W	0.43	0.32
		S	0.80	0.59
Post-smolt	3–5	S W S	0.05	–
Post-reproductive anadromous males		W S	–	0.10

Data were calculated from Murray (1968), Myers (1984), Hutchings and Myers (1986), Gibson *et al.* (1987) and
Bley and Moring (1988). (The post-smolt stage extends from the time individuals enter the sea, as smolts, to the
time of reproduction in fresh water.)
W, winter (October–April); S, summer (May–September).

laboratory (Hutchings and Myers, 1988) to calculate the fitness, *r*, associated with the parr and
anadromous strategies. The resultant fitness functions predict that, among populations, the
frequency of the parr strategy should increase with individual growth rate. Within populations,
age-specific variation in the shapes of the fitness functions (generated by phenotypic plasticity in
age at maturity) suggests that the fitness of each strategy is best represented as a three-
dimensional surface whose boundaries encompass natural variation in age at maturity and mate
competition. The points at which the fitness surfaces for each strategy intersect define an
evolutionarily stable continuum along which the fitnesses associated with each strategy are equal.
We propose a simple threshold model that incorporates polygenic thresholds of a largely
environmentally-controlled character (age at maturity) to account for the maintenance of
evolutionarily stable continua within populations.

Materials and methods

Fitness was calculated as *r*, the intrinsic rate of natural increase, using the discrete-time version of
the Euler–Lotka equation

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

where l_x is the probability of surviving from zygote to the beginning of the breeding season at age
x and m_x is the number of female zygotes produced by an individual aged *x*. For male Atlantic
salmon, m_x represents the number of eggs produced by a single female that were fertilized by a
male of age *x*. Age is calculated from time of fertilization in October/November so that integer
values of age represent ages at the beginning of the reproductive period.

Age-specific survival probabilities were calculated largely from a single Newfoundland
population, the Little Codroy River (Table 1). Annual survival probabilities of immature and
mature male parr were available from Myers (1984) and, following Hutchings and Myers (1986),
overwinter survival for immature parr was estimated to be 80% of their annual survival. The
increased mortality of mature parr relative to immature parr of the same age (see Myers, 1984)
was divided equally between summer (May–September) and winter (October-April). Survival at
sea prior to initial reproduction as an anadromous male was estimated as 0.05, the mid-range of
the estimates provided for the Little Codroy River population by Murray (1968). On average, we

assumed that 10% of post-reproductive anadromous males would survive to breed a second time 1 year later (Bley and Moring, 1988). Survival from the zygote to the end of the first summer of life was estimated as 0.27 by assuming that each anadromous female replaces herself at equilibrium. This estimated parameter is within previously reported survival rates of juveniles during the first year of life (Bley and Moring, 1988).

Strategy-specific fertilities were based on a laboratory manipulation experiment. Using genetic markers, Hutchings and Myers (1988) calculated the proportion of a female's brood that was fertilized by parr and by a single anadromous male under different parr densities (hereafter, referred to as parr frequency because of the direct association between the mean number of parr per female and the incidence of parr maturity within a population). These laboratory-based fertilization rates (1–29% for parr) correspond to estimates made under natural conditions (1–28%; Jordan and Youngson, 1992). We used Michaelis–Menton functions that describe parr fertilization success as a function of parr frequency (see Hutchings and Myers, 1988) to estimate the mean fertilization success of parr and anadromous males per brood (Fig. 1).

In calculating the fitness functions, we assumed that (1) males mature either as parr or as anadromous fish, i.e. there is no switching from the parr to the anadromous strategy (typically < 10% of parr switch in Newfoundland populations (e.g. Hutchings, 1985; Myers and Hutchings, 1986) and those that do probably suffer at least a 50% higher mortality at sea compared with males that do not mature as parr (calculated from Berglund *et al.*, 1992)), (2) anadromous males reproduce following 1 year at sea (valid for the majority of Newfoundland populations (Ash and O'Connell, 1987)), (3) one anadromous male is present per anadromous female (based on observations in semi-natural breeding experiments (I.A. Fleming, personal communication)), (4) all males, on average, have equal probability of mating (note that this does not imply that both forms of males fertilize equal numbers of eggs; cf. Hutchings and Myers (1988)), (5) the number of parr per female, i.e. parr frequency, ranges from 1 to 25 (based upon C. Garcia de Leaniz and F.A. Huntingford, unpublished data), (6) neither age nor body size influences parr fertilization success (violation of this assumption does not affect the qualitative results given here) and (7) each female produces 3000 eggs.

The fitness of male Atlantic salmon is based primarily on their 'decision age' at maturity. We assumed that there is a specific time of year during which males may 'decide' to mature as a parr or as an anadromous male (Thorpe (1986) provides a discussion of such critical periods). We assumed that this critical period occurs during May/June, the months of highest invertebrate abundance (salmonid food resource) in northern boreal rivers (Power, 1980) and we used decision ages 1.5, 2.5, 3.5 and 4.5 years to reflect natural variability in age at maturity. Importantly, males of the same decision age but opting for different strategies have ages at maturity which differ by 2 years. Those that 'decide' at age $x.5$ years to adopt the parr strategy reproduce initially in the autumn at age $x + 1$ years while those that 'decide' at the same age to adopt the anadromous strategy will migrate to sea the following spring as smolts, spend 1 year at sea and return to the river to reproduce initially at age $x + 3$ years.

Results

Age-specific variation in equilibrium parr frequencies

The fitness of males adopting the parr and anadromous strategies depends on parr frequency and decision age at maturity (Fig. 2). The fitness of the parr strategy declines rapidly with increasing parr frequency although the rate of decline decreases with increasing decision age at maturity. The fitness of the anadromous strategy is relatively unaffected by parr frequency. Regardless of parr frequency, the fitness of the anadromous strategy declines with increasing age at maturity

and the same is generally true for the parr strategy (the functions at ages 3.5 and 4.5 years overlap for a minority of parr frequencies). The points of intersection for each of the four age-specific sets of fitness functions indicate the parr frequencies at which the fitnesses associated with each strategy are equal. These equilibrium parr frequencies decline with increasing age at maturity from 22 to 4.5 parr per female, corresponding to decision ages 1.5 and 4.5 years respectively.

Within-population variation in strategy-specific age at maturity

When age at maturity varies within strategies, the fitness of parr and anadromous males is more appropriately represented as a three-dimensional surface whose boundaries encompass natural
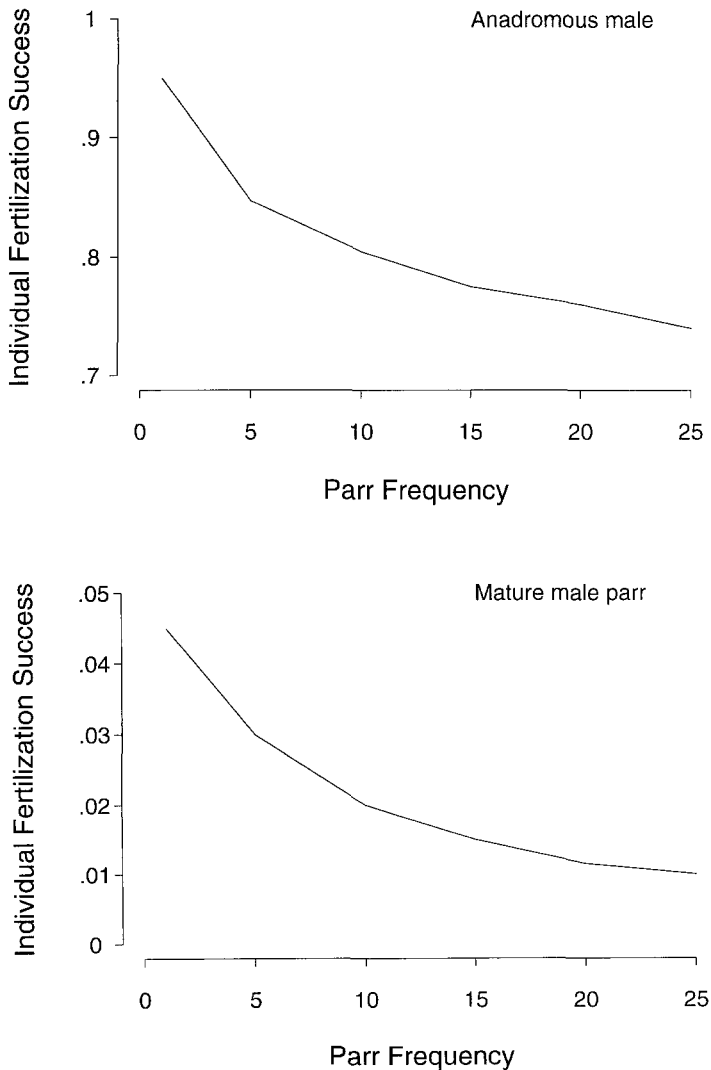

Figure 1. Estimated proportion of eggs in a single brood fertilized by individual anadromous male Atlantic salmon and by mature male parr (competing with a single anadromous male) for varying numbers of parr per female (parr frequency). Data were calculated from Hutchings and Myers (1988).

variation in age at maturity and mate competition (Fig. 3). (The surfaces in Fig. 3 represent interpolations of the data in Fig. 2.) The points at which the fitness surfaces intersect define an evolutionarily stable continuum (ESC) of frequencies along which the fitnesses associated with each strategy are equal.

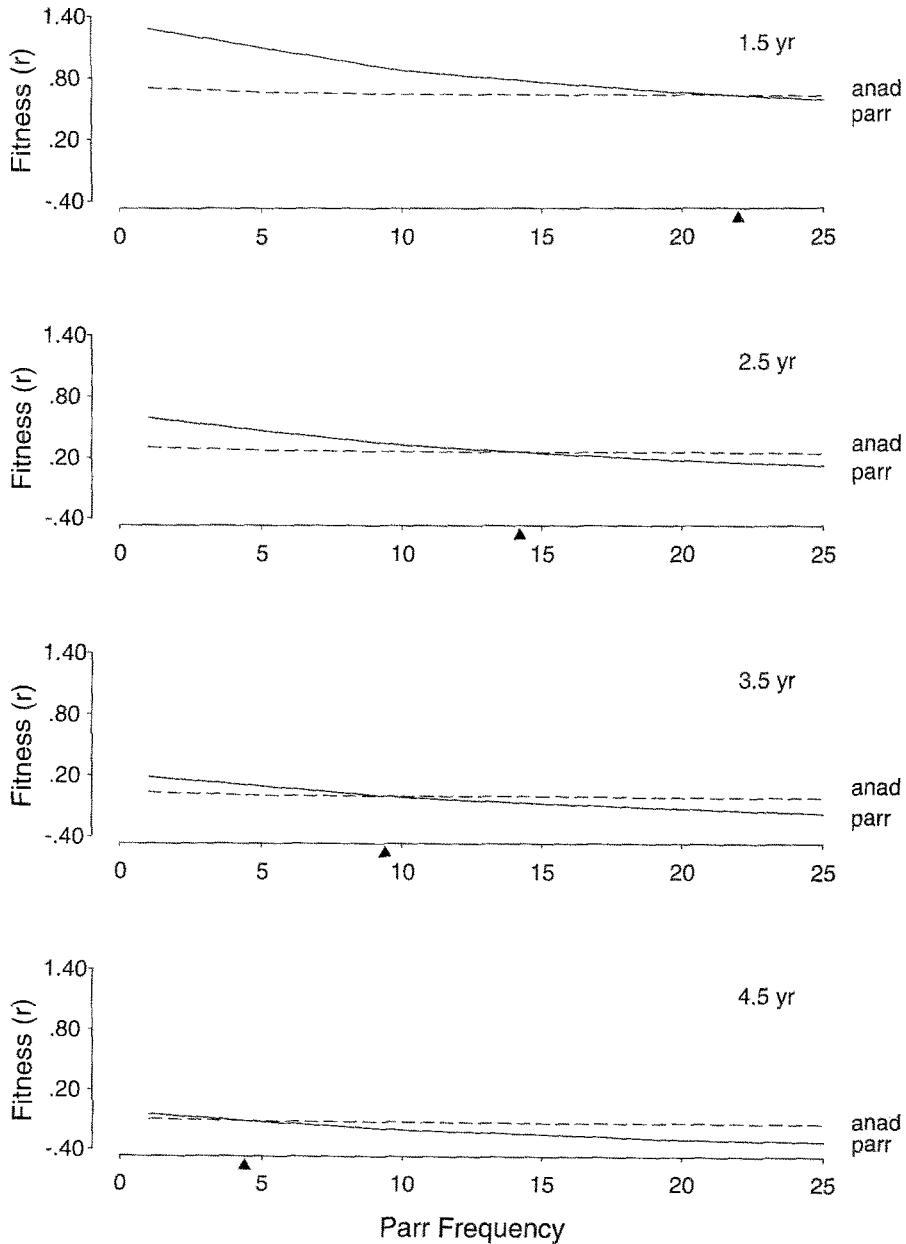The shapes of the fitness surfaces suggest that when early maturity is favoured (as it would be

Figure 2. The fitness (*r*) of anadromous male Atlantic salmon (dashed lines) and mature male parr (solid lines) as functions of parr frequency (numbers of parr per female) and decision age at maturity (defined in text). Equilibrium parr frequencies (indicated by solid triangles) decline with increasing age at maturity.

for relatively fast-growing individuals), individuals should generally, but not always (because of negative frequency dependence), mature as parr. However, the relative fitness benefits of maturing as a parr decline with increasing age at maturity (and progressively slower growth).

A threshold model of phenotypic plasticity in alternative reproductive strategies

We propose a model that incorporates polygenic thresholds (cf. Falconer, 1989; Hazel *et al.*, 1990) of a largely environmentally-controlled character (age at maturity) to provide a mechanism by which evolutionarily stable continua are maintained within populations (Fig. 4). We assume that there exist growth-rate thresholds which must be exceeded at a specific time of year before an individual will mature either as an anadromous male or as a mature male parr (cf. Thorpe, 1986). The notion that growth-rate thresholds are involved in parr maturation has been suggested by Leonardsson and Lundberg (1986) and by Bohlin *et al.* (1990). Individual variability for parr maturation can be described as genetic variability in parr maturation thresholds. Thus, we assume that there are two genotypes (α-males and β-males), each of which is characterized by a different parr maturation threshold and that the threshold of α-males exceeds that of β-males. Following Myers and Hutchings (1987), we assume that maturation is a polygenic character that can be modelled as a threshold trait. That is, a male either matures at a given age or it does not although maturation is undoubtedly controlled by more than one gene. Despite being phenotypically discrete, threshold traits can be modelled as quantitative characters by assuming they have underlying normal distributions for 'liability' (Falconer, 1989).

The distribution of age-specific growth rates is assumed to be normal with mean growth rate declining with increasing juvenile age (1.5–3.5 years) (Fig. 4). The growth-rate thresholds for
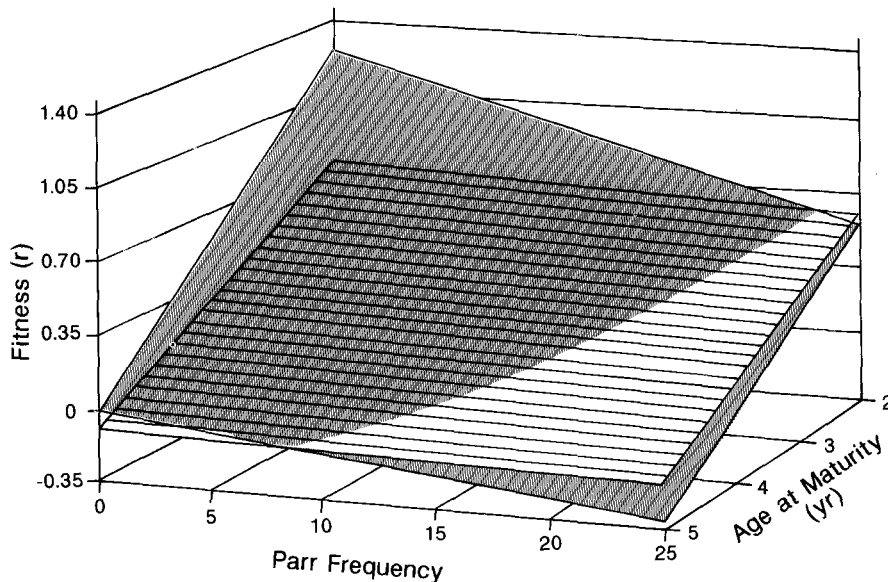

Figure 3. Fitness surfaces for alternative mating strategies in male Atlantic salmon (mature male parr, dark surface; anadromous males, light surface). Each surface describes the fitness (*r*) associated with maturing as a parr or as an anadromous male as functions of decision age at maturity (years) and parr frequency (numbers of parr per female). The intersection of the surfaces defines an evolutionarily stable continuum (ESC) along which the fitness of individuals adopting each strategy are, on average, equal. The surfaces represent interpolations of the data in Fig. 2. Thus, the parr frequencies along the ESC include the evolutionarily stable frequencies indicated by triangles in Fig. 2.
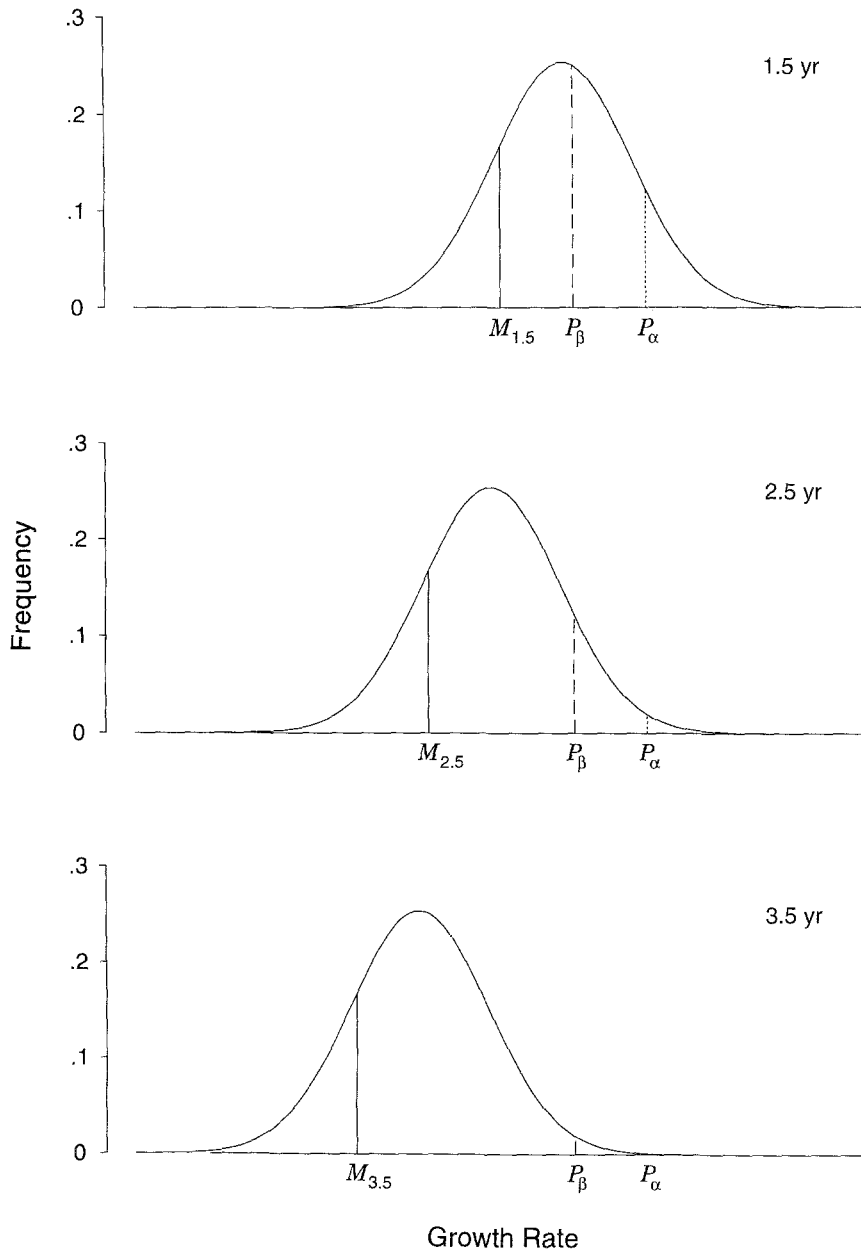
Figure 4. Model for the maintenance of evolutionarily stable continua in alternative mating strategies in male Atlantic salmon. Growth rate is normally distributed at three decision ages at maturity (1.5, 2.5 and 3.5 years). Growth-rate thresholds for parr maturation, P, (for α- and β-genotypes) are fixed at each age; growth-rate thresholds for maturation, M_x, decline with increasing decision age x. Males whose growth rate exceeds M in spring will mature as parr in the autumn if their growth rate exceeds the P threshold corresponding to their genotype. If growth rate exceeds M but not that genotype's P threshold, the male will migrate to sea the following spring and spend 1 year at sea prior to maturation as an anadromous male. Note that among the fastest growing males at each age, the probability of adopting the parr strategy declines with increasing age.

parr maturation (P_β for β-males and P_α for α-males) are fixed across ages. Alternatively, the maturation threshold, M_x, is assumed to decline with increasing decision age at maturity, x. Such a decline is reasonable when a minimum absolute level of energy reserves (e.g. lipids) is required for the physiological processes associated with seaward migration to occur. Thus, even though some individuals grow slowly for several years, they may have accumulated reserves sufficient to enable them to migrate to sea (their older age making it non-adaptive to mature as a parr). An age-specific decline in the M threshold also seems reasonable given that all surviving individuals within salmonid populations, regardless of growth rate, will eventually mature.

We assume that the 'critical' time period during which the M and P thresholds must be exceeded is spring and that growth rate is random with respect to the β- and α-male genotypes. Juvenile males exceeding the M threshold, but not one of the P thresholds, will migrate to sea the following spring and mature as anadromous males. Those whose growth rates exceed the P threshold associated with their genotype will mature as parr in the autumn. In the present example (Fig. 4), of the β-males whose growth rate exceeds M, 59% will reproduce as parr at age 2 years, 18% will mature as parr at age 3 years, but only 2% will do so at age 4 years. For α-males exceeding M in spring, 82% will reproduce as anadromous males at age 4 years, 98% at age 5 years and 100% at age 6 years. Thus, the model assumes that variation in the age-specific adoption of a given strategy is regulated by the age-specific decline in growth rate common to most organisms (cf. Needham, 1964; Ricker, 1975) and it predicts a higher incidence of parr maturity among young mature males and a lower incidence among older mature males, as predicted by the shape of the evolutionarily stable continuum in Fig. 3.

Discussion

The hypothesis that alternative mating strategies in male Atlantic salmon are maintained by negative frequency-dependent selection is supported by the observation that the predicted evolutionarily stable parr frequencies are within the range of frequencies observed in natural populations. One prediction that arises from the analysis is that evolutionarily stable frequencies of parr maturation decline with increasing age at maturity (cf. Fig. 2). Assuming that increased juvenile growth rate reduces age at maturity (Stearns and Koella, 1986; Thorpe, 1986; Hutchings, 1993a), this decline in equilibrium parr frequency provides a theoretical basis for the observation that populations comprised of fast-growing individuals have a higher incidence of parr maturation than populations comprised of slow-growing individuals (Myers *et al.*, 1986). The age-specific decline in frequency equilibria can be attributed to the diminishing importance of juvenile (i.e. pre-reproductive) survival and age at maturity to fitness. Despite fertilizing relatively few eggs, parr achieve large fitness gains by maturing early and, thus, by coupling low juvenile mortality with a high rate of gene turnover. But with increasing age at maturity, differences in maturation age and juvenile survival between parr and anadromous males decrease progressively, resulting in an age-specific decline in parr fitness relative to that of anadromous males.

The fitness of a reproductive strategy in a variable environment is best represented as a multidimensional surface. This is because phenotypic plasticity in age at maturity, effected by environmental heterogeneity in the prospects for individual growth, is associated with age-specific differences in the fitness consequences of adopting a given strategy. In male Atlantic salmon, the shape of the evolutionarily stable continuum (which delineates the points of intersection of the strategy-specific fitness surfaces) suggests that fast-growing, early-maturing males are generally favoured to adopt the sneaker, parr strategy whereas slower-growing, later-

maturing males are generally favoured to adopt the behaviourally-dominant, anadromous strategy. The evolutionarily stable continuum exists because of negative frequency-dependent selection and its shape would be predicted to vary with both population demography (i.e. age-specific rates survival and fecundity) and with environmental variability in the opportunities for individual growth.

We have proposed a model for phenotypic plasticity in alternative strategies in which we assume (1) that juvenile growth rate is random with respect to genotype, (2) that increased juvenile growth rate favours earlier maturity, (3) that maturation is dependent upon the attainment of a critical growth rate and (4) that different growth-rate thresholds exist for adoption of the parr and anadromous strategies. We predict that selection will optimize threshold traits relative to the variability in the age-specific growth rate that individuals can expect to experience from one generation to the next. Thus, maturation thresholds for alternative strategies should differ among populations that are subjected to different levels of environmental variability in growth rate.

Our model makes several predictions: (1) growth-rate thresholds are polygenic traits whose values depend upon (i) the relative fitness of the parr and anadromous strategies and (ii) on the environmental variability in growth rate experienced by individuals from one generation to the next, (2) populations comprised of fast-growing (i.e. early-maturing) individuals should have a higher incidence of parr maturity than populations comprised of slow-growing (i.e. late-maturing) individuals (supported by field data on 28 Canadian populations (Myers *et al.*, 1986)), (3) the fastest growing progeny of *both* anadromous males and mature male parr should adopt the parr strategy although the overall incidence of parr maturity should be greater among the progeny fathered by parr (supported by laboratory data provided by Thorpe *et al.* (1983)) and (4) frequency-dependent selection maintains the frequencies of the α- and β-genotypes, *not* the frequencies of the parr and anadromous strategies, in an evolutionarily stable state through selection on the growth-rate thresholds for parr maturation (cf. Fig. 4).

Growth-rate thresholds for maturation and their maintenance by stabilizing selection can be assessed indirectly within natural populations. If thresholds for parr maturation are normally distributed among genotypes within a single population, then a random sample of males throughout that distribution should yield a normal cumulative density function of parr maturation against body size for males of the same age (cf. Hazel *et al.*, 1990). For example, assume that parr maturation thresholds are normally distributed about a mean size of 75 mm at age 2 years (Fig. 5A). Among a sample of age 2 year males within such a population, none of the males < 60 mm will have reached their threshold for parr maturation and all such males should be immature. Among the 75 mm males, 50% will have attained or exceeded their thresholds and 50% will mature as parr. Similarly, all males > 90 mm will have attained or exceeded their thresholds and all will mature as parr. Among a large ($n=1275$) sample of age 2 year males from the Little Codroy River, Newfoundland – the only population for which such data are available – the relationship between incidence of parr maturity and body size fits a normal cumulative density function (Fig. 5B). These data are consistent with the hypothesis that thresholds for maturation exist and are maintained by stabilizing selection. This hypothesis appears to have general validity across a diverse array of taxa. Hazel *et al.* (1990) also found general agreement between the predictions of their model of polygenic threshold traits and empirical data on conditional strategies in acorn barnacles, *Chthamalus anisopoma*, swallowtail butterflies, *Papilio polyxenes* and coho salmon, *Oncorhynchus kisutch*.

The inability of genotypes to control the dispersal of their offspring across spatially heterogeneous environments should favour adaptive phenotypic plasticity in life history. The influence of plasticity in the maintenance of alternative mating strategies can be assessed by

modelling fitness as a multidimensional surface and by assuming that the adoption of a given strategy is dependent upon age and upon an individual's local environment. Evolutionarily stable continua, maintained by frequency-dependent selection on threshold traits, provide a theoretical basis for understanding how life histories evolve in variable environments.
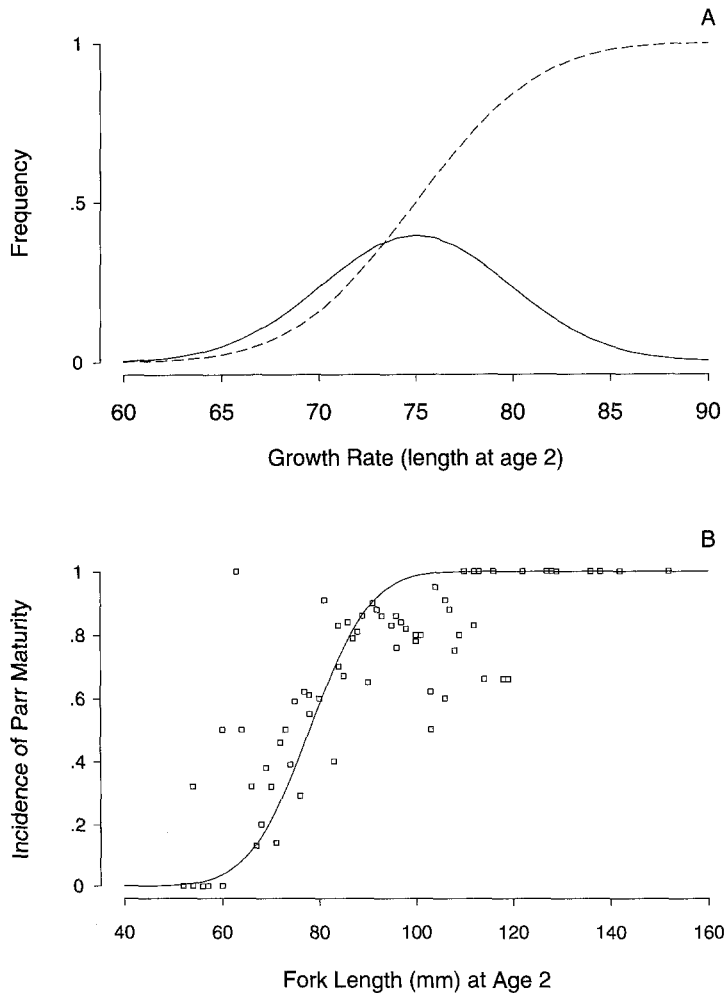
Acknowledgements

Figure 5. Indirect test for the existence of growth-rate thresholds for parr maturation. (A) If thresholds (approximated by size at age 2 years) are normally distributed (solid curve) within populations (as would be expected under stabilizing selection), then the incidence of parr maturity among age 2 year males throughout that range of growth rates should follow a normal cumulative density function (dashed curve). (B) Evidence of a cumulative density function for parr maturation against growth rate for age 2 year males from the Little Codroy River, Newfoundland (data redrawn from Myers *et al.*, 1986).

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