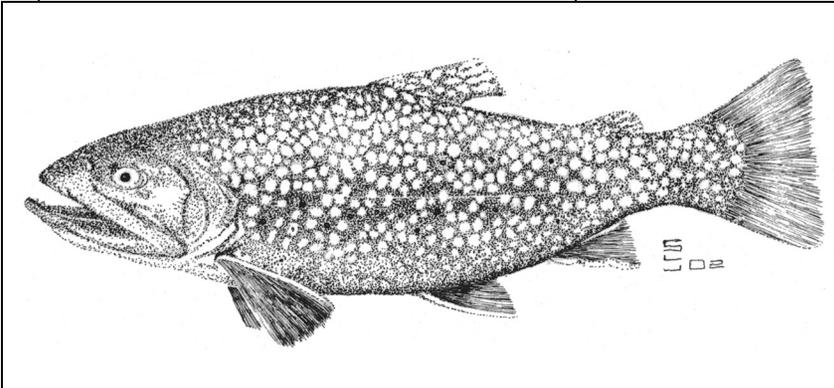


Norms of Reaction and Phenotypic Plasticity in Salmonid Life Histories

Jeffrey A. Hutchings



Mature male brook trout

5

Theory predicts that adaptive plasticity in life history strategies should be favored in organisms with widely dispersed offspring because of the increased likelihood of encountering spatial and temporal environmental heterogeneity. Phenotypic plasticity is the ability of a genotype to produce different phenotypes across an environmental gradient (Bradshaw 1965; Schlichting and Pigliucci 1998; Debat and David 2001). Plasticity does not represent genetic change, although the form of change (the trait may increase in value, decrease, or remain the same) may be a product of selection. Phenotypic plasticity can be heuristically and graphically described as a norm of reaction, a linear or nonlinear function that expresses how the phenotypic value of a trait for a given genotype changes with the environment (Schmalhausen 1949; Schlichting and Pigliucci 1998).

The primary purpose of this chapter is to explore the adaptive basis of plastic changes in salmonid life history traits, to examine how norms of reaction have been used to explain the persistence of life history variation among individuals within populations, and to hypothesize how selection, including that induced by anthropogenic activities such as fishing, might change the shapes of reaction norms, thereby influencing how individuals within populations respond to environmental change. Within the context of evolutionary biology, one of the themes that emerges from the study of reaction norms in salmonids is the need to determine how fitness changes as genotypes alter their phenotype along different reaction norms, a subject that has received little attention to date.

Life history strategies describe how genotypes vary their stage- or age-specific expenditures of reproductive effort in response to intrinsic and extrinsic factors that influence survival and fecundity. As such, life histories reflect the expression of traits most closely related to fitness, such as age and size at maturity, offspring size and number, and longevity, as well as the timing of the expression of those traits throughout an individual's life. Implicit within any life history theory prediction is the assumption that natural selection favors those genotypes whose age(stage)-specific schedules of survival and fecundity generate the highest per capita rate of increase, that is, fitness, relative to other genotypes in the same population (Stearns 1992; Roff 2002). This genotypic rate of increase can be expressed as r , the intrinsic rate of natural increase, or as R_0 , the net reproductive rate. When expressed at the individual level, r and R_0 represent fitness. When expressed at the population level, they represent rates of population growth, parameters that determine extinction probability, recovery rate, and sustainable levels of exploitation. From an evolutionary perspective, it is reasonable to focus on life history traits because of the direct link that exists between these characters and fitness.

When life history trait optima differ among environments inhabited largely at random with respect to genotype within and among generations, selection can be expected to act on the way in which a genotype alters its life history in response to environmental change. That is, selection will act on a genotype's norm of reaction (Schmalhausen 1949; Via and Lande 1985; Schlichting and Pigliucci 1998). Such adaptive phenotypic plasticity may underlie many life history responses by salmonid fish to environmental change, notably to non-

genetic variation in individual growth rate, but also to differences in temperature, habitat quality, and food supply. Random distribution of salmonid genotypes among spatially heterogeneous environments may be most likely in early life, almost immediately after individuals begin to feed exogenously. Upon emergence from gravel egg nests, many salmonids are transported to areas of slow-moving water where they spend periods of time ranging from days to months of their first growing season (Northcote 1984; Hutchings 1996; Marschall et al. 1998). It is likely that individuals utilize these habitats at random with respect to genotype because of: (1) the inability of recently emerged juveniles to swim against all but the weakest of water currents; (2) spatial and temporal variation in hydrography and food supply; and (3) significant discordance in emergence times among individuals from the same brood (e.g., Field-Dodgson 1988; Snucins et al. 1992).

Despite the voluminous life history literature on salmonids (Groot and Margolis 1991; Fleming 1996; Hutchings and Jones 1998; Marschall et al. 1998), only a handful of studies have focused on reaction norms for life history traits. Based on data for unexploited populations of brook charr in southeastern Newfoundland, Hutchings (1993a,b, 1996, 1997) constructed norms of reaction for age and reproductive effort at maturity, providing a basis for predicting how such plasticity might change under exploitation. Experimental studies have revealed how reaction norms for juvenile growth rate in brown trout (Einum and Fleming 1999) and juvenile survival in brook charr (Hutchings 1991) can be influenced by egg size, and there is corresponding evidence that growth rate in early life can negatively (N. Jonsson et al. 1996; Morita et al. 1999) and positively (Morita et al. 1999) influence egg size as an adult in Atlantic salmon and white-spotted charr, respectively. By modeling reaction norms as threshold traits, researchers have been able to account for the influence of both environmental and genetic influences on age at maturity when explaining the maintenance of conditional alternative mating strategies in Atlantic salmon (Hutchings and Myers 1994) and coho salmon (Hazel et al. 1990), and within-population differences in time spent at sea prior to reproduction (Hutchings and Jones 1998). The most recent work on life history reaction norms in salmonids, described in a series of papers on European grayling, has provided some of the most compelling evidence to date for the hypothesis that population differences in reaction norms represent adaptive responses to local environments (Haugen 2000a,b,c; Haugen and Vøllestad 2000).

1. Theory: Reaction Norms and Adaptive Phenotypic Plasticity

1.1. *Genotype* × *Environment Interactions*

Reaction norms describe how individuals respond to environmental change. Strictly speaking, within an evolutionary context, norms of reaction pertain to responses by genotypes, the units of study when Wolterreck (1909) first coined

the term *Reactionsnorm* in his work on *Daphnia*. Genotypic studies of reaction norms are not uncommon in plants, clonal organisms, and *Drosophila* (see Schlichting and Pigliucci (1998) for examples) because of the relative ease with which single genotypes can be generated and their responses to environmental change documented. However, for most sexually reproducing animals, the family level is the lowest level at which reaction norms can be studied.

Reaction norms inform us about the magnitude of trait plasticity, the presence of genotype \times environment ($G \times E$) interactions on the phenotypic expression of a given trait, and the extent to which the additive genetic variance (V_A) of a trait changes with the environment. Norms of reaction that run parallel to the environmental gradient axis reflect an absence of plasticity because the trait does not change its phenotypic value with changes in the environment (Figure 5.1A). Plasticity is reflected by reaction norms with non-zero slopes. In Figure 5.1B, the reaction norms have similar slopes, implying that the pattern of phenotypic response to environmental change is the same among genotypes, that is, there is no $G \times E$ interaction. In contrast, crossing reaction norms, indicative of $G \times E$ interaction, suggest the presence of genetic variation in plasticity (Figure 5.1C). If that genetic variation is additive, then selection can produce evolutionary changes to the shapes of reaction norms, thus making their study fundamentally important to evolutionary biology.

Genotype \times environment interactions can affect the degree to which alleles are subject to selection. For the reaction norms in Figure 5.1C, the differences in phenotype among genotypes are greatest at the environmental extremes; if that genetic variation is additive, one can conclude that the V_A of the trait in question will be highest at the extremes of the environmental gradient. By contrast, V_A will be much lower near the center of the environmental gradient, where the reaction norms converge, because of the similarity in phenotypic values among the different genotypes. Thus, the additive genetic variation of the trait in question, and the rate at which it will respond to selection, will vary with the environment.

1.2. Inferring Individual Responses to Environmental Change

Several approaches can be used to infer the shapes of reaction norms. In a broad sense, this is a hierarchical process of obtaining data on how the phenotypic values of life history traits change with the environment. At the highest level, one focuses on population means of a given life history trait, such as age at maturity, that are plotted against an environmental variable, such as temperature. The line best fitting these data (a “species-level” reaction norm) has frequently been used to identify how individuals within a population might respond to environmental change. Examples in the salmonid literature of such population-level variation for life history traits abound (Marschall et al. 1998), for instance, egg size and fecundity versus latitude (a proxy for environmental variation) in coho salmon (Fleming and Gross 1990); Atlantic salmon smolt age and metrics of growth rate (Power 1981; Metcalfe and Thorpe 1990; Hutchings and

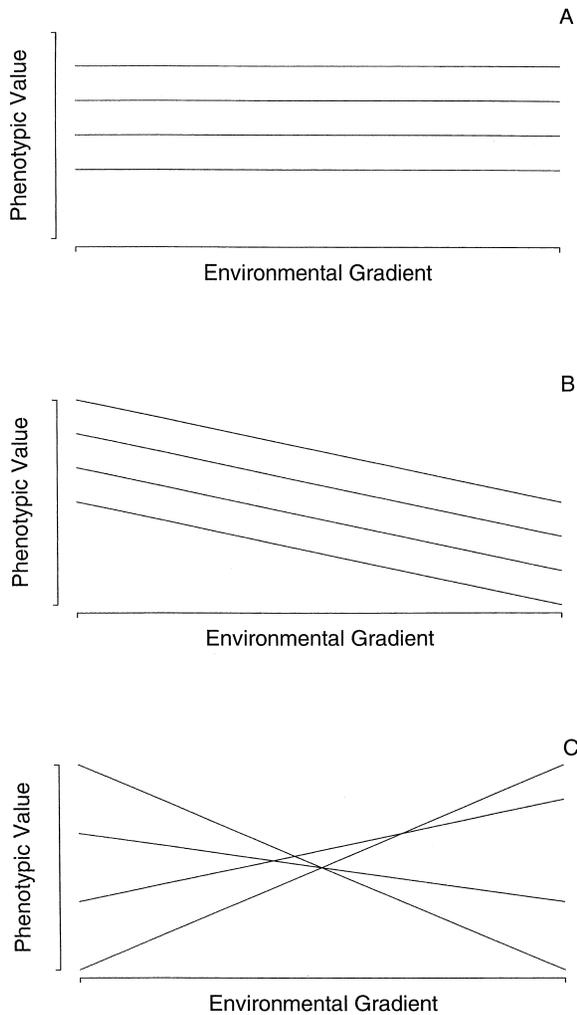


Figure 5.1. Reaction norms describe changes in the phenotypic value of a trait across an environmental gradient. Reaction norms can reflect an absence of plasticity (A), the presence of plasticity but an absence of genotype \times environment ($G \times E$) interactions (B), or the presence of both plasticity and $G \times E$ interactions.

Jones 1998); and incidence of the Atlantic salmon male parr maturity and growth rate (Myers et al. 1986).

Population-level functions represent the second level of the hierarchical process of identifying reaction norms, wherein each graphical relationship could be described as a “population-level” norm of reaction (Figure 5.2A). This approach can be useful if the primary goal is to predict how individuals within a population will respond, on average, to specific changes in an environmental variable. But the use of population-level data to infer individual

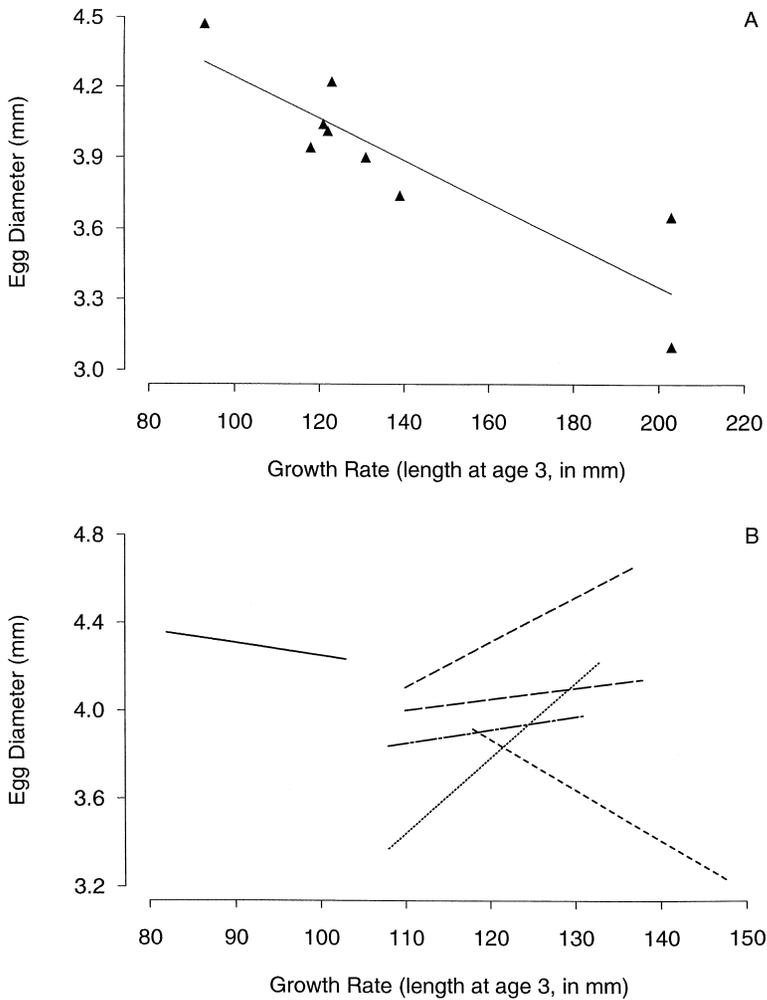


Figure 5.2. Bivariate plots of egg size against growth rate in brook charr reveal differences in the predicted associations between these traits when the correlations are calculated on the basis of population means within species (A) or among individuals within populations (B). The data presented in (A) are from Hutchings (1990); the data presented in (B) are from Hutchings (1990, 1996) and from Adams (1999).

responses to environmental change is subject to several statistical and biological caveats. For example, a plot of the average egg size against average individual growth rate (approximated by the mean length at age 3 years, a reasonable proxy for environmental variation) yields a significantly negative correlation among nine populations of brook charr ($r = 0.88$, $p = 0.0017$; Figure 5.2A; Hutchings 1990). However, when one plots the separate relationships between egg size and growth rate among individuals within populations, the correlation coefficients range from significantly negative to significantly positive (Figure 5.2B). The

observation that populations respond differently to changes in the environment is consistent with the hypothesis that individuals within such populations are, to some degree, adapted to their local environments.

The study of co-gradient and counter-gradient variation provides an excellent empirical and theoretical framework for the study of population differences in the average response by individuals to their environment (reviewed by Conover and Schultz 1995). Co-gradient variation describes heritable traits that vary genetically and phenotypically in a manner predicted by the environment (e.g., the most rapid genetically based growth is found among those individuals inhabiting the environment most favorable to growth). In contrast, counter-gradient variation exists when genotypes are distributed such that genetic and environmental influences on a trait oppose one another (e.g., the population exhibiting the fastest genetically based growth inhabits the environment least favorable to growth). The observation that populations in apparently hostile environments (cold temperature, low food) express the most rapid rates of growth across a range in environmental variables provides the most widely cited example of counter-gradient variation in fish (Conover and Schultz 1995). In salmonids, Nicieza et al. (1994) found evidence of counter-gradient variation in Atlantic salmon digestion rate. Although support for counter-gradient variation in growth rate was equivocal in a recent study in the same species, B. Jonsson et al. (2001b) were able to document population-level norms of reaction for rates of growth and food consumption in Atlantic salmon.

However, if one wishes to estimate the genetic variation in reaction norms within a population, assess the degree to which reaction norms are under selection, or predict the rate at which the shapes of reaction norms might change in response to selection, a finer-scale approach needs to be adopted. This third level of the hierarchy involves the study of plasticity of individuals from the same family. This is usually the lowest level of analysis at which one can use empirical data to describe the shapes of reaction norms in salmonids (for an example in which intra-individual variation is examined in salmonids, see Einum and Fleming 1999).

Although data on family-level responses to environmental change are commonly gathered in aquaculture breeding programs, relatively few have been reported in the primary literature. Among those, Beacham and Murray (1985) describe interfamilial variation in phenotypic responses to environmental change for chum salmon from Nitinat River, British Columbia, Canada. Reaction norms between embryonic survival and incubation temperature reveal considerable genetic differences among families (Figure 5.3A). This $G \times E$ interaction is reflected by families for which survival during the egg stage increases, remains constant, or declines with increases in incubation temperature from 4 to 12°C. The most common norm of reaction is one in which offspring survival is highest at the intermediate temperature. If the genetic variation among families is primarily additive (and if other genetic sources of variation do not change with temperature), then one would conclude that V_A for egg survival is highest at high and low temperatures, and lowest at 8°C. By comparison, reaction norms between length at emergence and temperature exhibit comparatively little

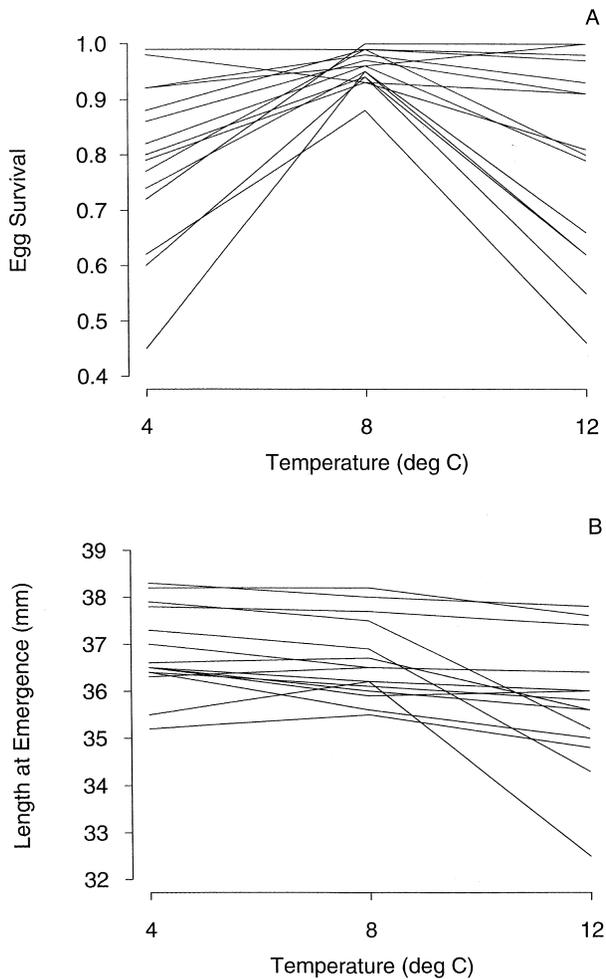


Figure 5.3. Differences in reaction norms for egg survival (A) and length at emergence (B), as functions of temperature, among families of chum salmon from the Nitinat River, British Columbia, Canada. Data were obtained from Beacham and Murray (1985).

genetic variation among families, as suggested by similarities in phenotypic response to environmental change (Figure 5.3B). This comparatively low level of $G \times E$ interaction occurs because reaction norms for alevin size fall primarily into only two types; size at emergence is either invariant with temperature or declines between 8° and 12°C.

On an explanatory note, attention should be drawn to the fact that studies of reaction norms in salmonid fish use growth rate as both a proxy for environmental change and as a trait in itself. When used in the former manner, growth rate is plotted on the abscissa and the trait whose reaction norm is being described is plotted on the ordinate. Although growth rate is generally a very

good metric of environmental change in indeterminately growing organisms, one need always be cognizant of the implicit assumption that size-at-age is a reliable proxy for growth. Use of growth rate as a metric for environmental change is common in field-based research and in studies for which the precise source of environmental variation is unknown. In contrast, reaction norms for growth rate, such as those presented in Figure 5.3B, are generally restricted to laboratory work. Also, it is not uncommon to have reaction norms depicted as bivariate plots between two life history traits, such as age and size at maturity (e.g., Stearns and Koella 1986). Whether these can truly be called reaction norms is perhaps open to debate, given that environmental change is not made explicit in such plots. However, what such bivariate associations do illustrate is the fact that life history tradeoffs, reflected by negative genetic and phenotypic correlations between traits, can differ among individuals within the same population. In this sense, they are analogous to, if not the same as, norms of reaction.

It is also worth underscoring the point that reaction norms in themselves tell us little about the fitness associated with genotypic responses to environmental change. Temperature, for example, can affect growth rate, which can then affect age at maturity, which may be positively or negatively associated with size at maturity, all of which can have consequences to reproductive effort. Thus, although always presented in two dimensions, reaction norms may often be hierarchical or n -dimensional in nature, reflecting the general observation that neither traits nor their reaction norms are independent of one another. It is this interdependence, mediated in part through lifehistory tradeoffs, that ultimately influences fitness.

2. Reaction Norms for Life History Traits in Salmonids

2.1. *Continuous Norms of Reaction for Age at Maturity: Individual and Population Variability*

The most widely reported association between a metric of environmental quality and a life history trait in fishes is that between individual growth rate and age at maturity. The observation that faster growers mature earlier in life has been documented repeatedly in the laboratory and in the field (Alm 1959; Hutchings 1993a; Roff 2002). However, it is not clear that this association is necessarily adaptive. Furthermore, changes in age at maturity probably have consequences to individual fitness and to population growth rate, both of which may influence the risk of extinction for the individual genotype and the population as a whole. Changes in r brought about by plastic changes in genotype could have important consequences to the conservation biology and sustainability of commercial and non-commercial species.

To evaluate the adaptive significance of phenotypic plasticity in age at maturity in brook charr, Hutchings (1996) examined how environmental variation in juvenile (pre-reproductive) growth rate can generate variation in fitness (r) across a range of potential ages at maturity. The empirical data were obtained

from three populations located on Cape Race, southeastern Newfoundland, Canada (these populations have been described in detail elsewhere; Hutchings 1993a,b, 1994, 1997). In many respects, the Cape Race trout populations are ideally suited for ecological and evolutionary study. The populations are unexploited and have not been subject to anthropogenic disturbance. Brook charr are the only fish in the rivers and they are not subject to avian predation, negating the potentially confounding influences of interspecific competition and predation on life history. In addition, these non-anadromous populations, despite being in close geographic proximity to one another, are genetically distinct, with some allozyme loci having reached fixation (Ferguson et al. 1991). In addition to the relative physical and biological simplicity of these systems, extensive life history data have been collected for these trout, including information on age-specific survival and fecundity, egg size, growth rate, age and size at maturity, and longevity (Hutchings 1993a,b, 1994, 1996, 1997).

Individual variation in brook charr growth rate prior to maturity is associated with significant variation in overwinter survival and fecundity; smaller individuals experience higher overwinter mortality and lower fecundity than larger individuals (Hutchings 1994, 1996). (The implicit assumption that size-at-age is a reasonable approximation of growth rate for these trout is based on similarity in size-at-emergence and length of growing season among years; J. Hutchings unpublished.) The primary consequence of this variation in growth is a substantial range in predicted fitness among individuals who reproduce early in life (3 years of age for two populations, 4 years for the third study population). This raises the question of whether slower-growing individuals, because of the fitness costs associated with maturing at a small size, might be favored to delay maturity, continuing to allocate energy to somatic growth rather than gonadal development. Using optimality theory, Hutchings (1996) predicted the fitness consequences associated with different ages at maturity and different rates of juvenile growth (Figures 5.4A,B), permitting the construction of norms of reaction for age at maturity for each population (Figure 5.4C).

With respect to these reaction norms, two observations are of note. First, the fitness functions support the prediction that a reaction norm describing a negative association between growth rate and age at maturity can represent an adaptive plastic response to environmental change. In Watern Cove and Cripple Cove populations, the slowest growing females are predicted to maximize fitness by delaying maturity, while the fastest growing individuals maximize fitness by maturing early in life.

Second, reaction norms for age at maturity are predicted to differ among populations (Figure 5.4C). In contrast to females in Watern Cove and Cripple Cove populations, those in Freshwater River are favored to mature early in life, regardless of growth rate. This underscores the point that the fitness advantages of delaying maturity (increased fecundity and higher overwinter survival because of larger body size) are inevitably balanced by the probability of realizing those benefits. Compared to trout in the other two populations, Freshwater River adult females experience significantly higher overwinter mortality (87%, as compared with 64% and 60% in Watern Cover and Cripple Cove Rivers, respec-

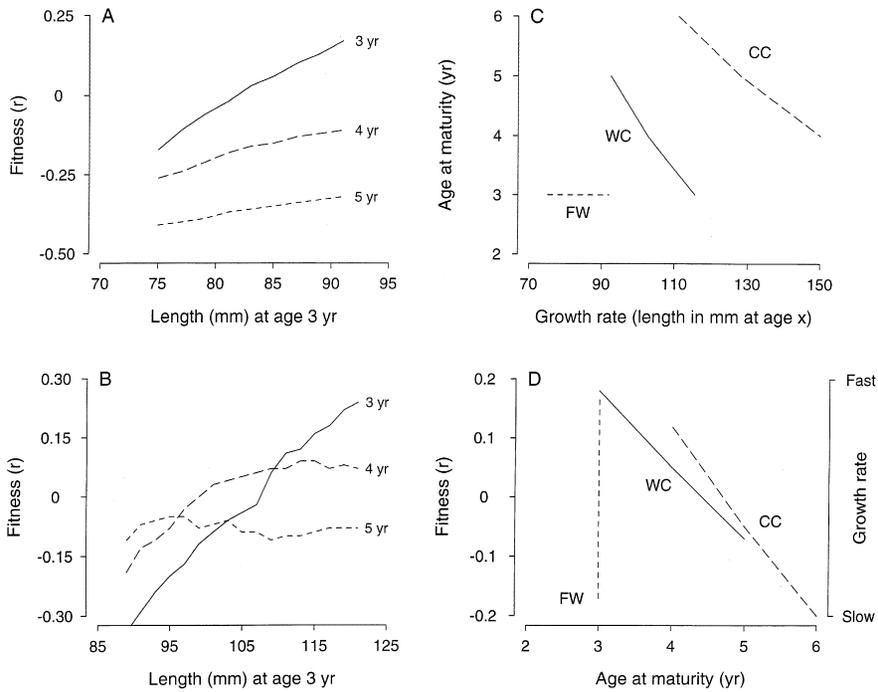


Figure 5.4. Fitness functions and reaction norms for age at maturity in populations of brook charr from Cape Race, Newfoundland, Canada. Associations between fitness at three ages at maturity are presented for females in Freshwater River (A) and Watern Cove River (B). Reaction norms for age at maturity as a function of individual growth rate are presented in (C) for females in Freshwater River (FW), Watern Cove River (WC), and Cripple Cove River (CC). Predicted changes to fitness (r), as phenotypes change along the norms of reaction presented in (C), are given in (D). (Note that growth rate on the right ordinate is a qualitative representation of the lengths at age given in (C); one should not interpret growth rate as being perfectly correlated with fitness.)

tively) and considerably slower growth in the wild (Hutchings 1993a, 1994). Thus, Freshwater River females appear to be favored to mature early in life, regardless of growth rate, because the survival costs of delaying maturity are too high relative to the apparently marginal benefits of increased fecundity.

Combining the information on fitness, age at maturity, and growth rate, one can assess the degree to which fitness (r) changes as individuals alter their phenotype (age at maturity) across an environmental gradient (reflected here by changes to individual growth) (Figure 5.4D). The primary point is that fitness can change as individuals alter their phenotypes along norms of reaction, an association all too rarely quantified in studies of plasticity. Thus, plastic changes in individual phenotypes can potentially have significant effects on the conservation biology of populations, affecting both their resilience and their ability to respond adaptively to environmental change.

Population differences in reaction norms for age, and size, at maturity have also been documented in grayling. Haugen (2000b) provided evidence of negative reaction norms between growth rate and age at maturity within four populations in Norway. Interestingly, however, he also found evidence of a non-plastic reaction norm for female grayling in one population, Øvre Mærrabottvatn, similar to that described above for Freshwater River brook charr. Regardless of growth rate, Øvre Mærrabottvatn grayling mature at 3 years of age, as compared to 4 to 8 years for grayling in the other populations. Haugen (2000b) attributed this invariant reaction norm in Øvre Mærrabottvatn grayling to the significantly higher mortality experienced by individuals in this population, during both the juvenile and adult stages, relative to that in the other populations. Given the recent common ancestry of the five populations (Haugen 2000a,b,c), this raises the possibility that the present invariant reaction norm observed for Øvre Mærrabottvatn grayling may represent a selective response to higher rates of mortality, a hypothesis discussed in more detail below.

2.2. Reaction Norms as Threshold Traits: Alternative Mating Strategies

Reaction norms need not vary continuously along an environmental gradient. This may be particularly true of those that underlie discontinuous variation in life history within populations. One example of discontinuous variation in salmonids is that of alternative maturation phenotypes within single populations (Gross 1985; Maekawa and Onozato 1986; Marschall et al. 1998). Male Atlantic salmon, for example, mature either as large (45–90 cm), relatively old (4–7 years) anadromous individuals, or as small (< 7–15 cm), young (1–4 years) mature parr (Jones 1959; Hutchings and Myers 1994; Metcalfe 1998; Fleming and Reynolds 2003—*this volume*). The former attain maturity following migration to sea (although some may have previously matured as parr), the latter do not. Prior to spawning, dominant anadromous males defend access to an anadromous female, while mature male parr establish what appears to be a size-based dominance hierarchy immediately downstream of the courting anadromous fish (Jones 1959; Myers and Hutchings 1987b). Mature parr compete with one another and with anadromous males for the opportunity to fertilize eggs. Since the first estimates of fertilization success in Atlantic salmon (Hutchings and Myers 1988), several studies have documented substantial reproductive success by parr as a group (e.g., Jordan and Youngson 1992) and as individuals (e.g., Thomaz et al. 1997), including recent estimates of the variance in individual fertilization success (Jones and Hutchings 2001, 2002).

The persistence of alternative mating “strategies” (or “tactics”, depending on the interpretation, Cross 1996) has been explained as a product of negative frequency-dependent selection (Partridge 1988). As the frequency of a given strategy increases within a population, increased competition among individuals adopting that strategy will experience reduced average fitness. By contrast, the average fitness of individuals adopting the alternative strategy would increase

because of reduced competition, resulting in a shift to the alternative strategy within the population.

There is good evidence that alternative mating strategies in salmonids have a genetic basis. Comparing the incidence of jacking (early maturity) among male progeny sired by jacks and by “hooknose” (late-maturing) chinook salmon, Heath et al. (1994) estimated the heritability of jacking to be about 0.4. Two studies have compared the incidence of male maturity as parr and as one-sea-winter Atlantic salmon, or grilse, among different families from several populations (Glebe and Saunders 1986; Herbinger 1987). Despite being reared in the same environment, the incidence of parr and grilse maturity differed significantly among families in both studies (Figure 5.5A), providing strong evidence of a

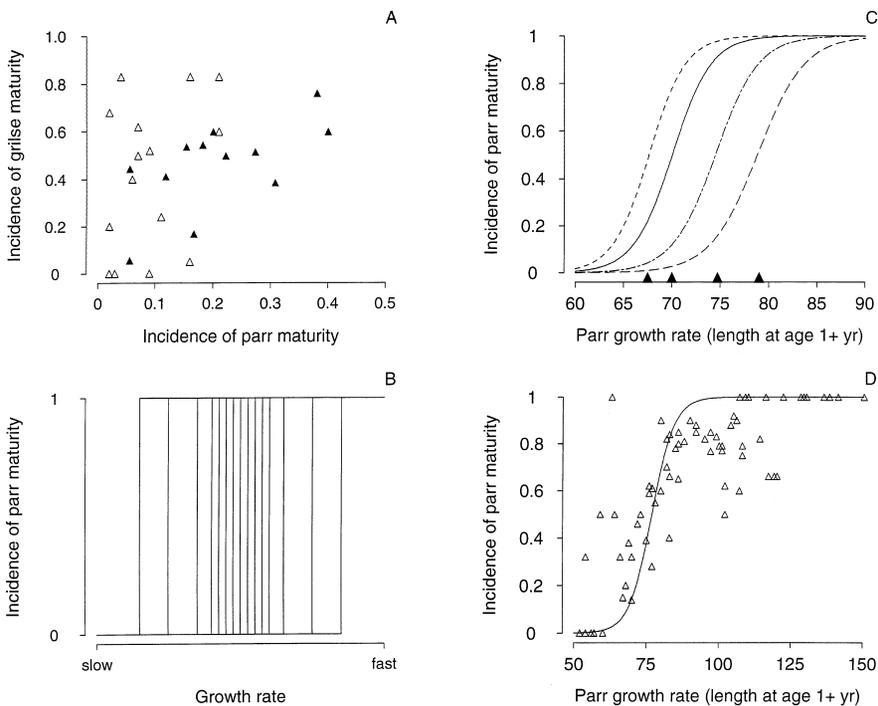


Figure 5.5. Genetic variation for alternative mating strategies in salmonids and the modeling of age at maturity reaction norms as threshold traits. (A) Genetic differences in the incidence of Atlantic salmon parr maturity are suggested by differences in age at maturity among families (represented by different points) reared under the same environmental conditions (solid triangles represent data from Herbinger (1987); open triangles are data from Glebe and Saunders (1986)). (B) Threshold reaction norms for age at maturity, redrawn from Hazel et al. (1990). (C) Hypothesized differences among populations in norms of reaction for Atlantic salmon parr maturity. Solid triangles represent the lengths at age at which 50% of the male parr in each population would be expected to adopt the parr reproductive strategy. (D) Incidence of male parr maturity plotted against individual growth rate for Atlantic salmon parr in the Little Codroy River, Newfoundland (redrawn from Myers et al. 1986).

genetic basis for parr maturation, notwithstanding maternal effects (which could not account for the observed variation). Breeding experiments also suggest that the incidence of parr maturity is higher among the progeny of mature male parr than it is among those of anadromous males (Thorpe et al. 1983; Gjerde 1984a; Glebe and Saunders 1986).

Whatever the genetic basis to parr maturity, it is clear that environmental factors are also of significant importance. In particular, there is a significant correlation between growth rate and/or condition and the likelihood of maturing as parr (Myers et al. 1986; Thorpe 1986; Bohlin et al. 1994; Metcalfe 1998). Given that much of this variation in growth rate/condition is environmental in origin (e.g., broad-sense heritabilities for growth rate in the first year of life are typically between 0 and 0.2 for salmonids; Kinghorn 1983; Nilsson 1994), there is a need to explain how genetically influenced alternative strategies can be evolutionarily stable within populations that also experience environmental heterogeneity largely at random with respect to genotype, and for which habitat quality significantly influences fitness.

Thus, it would seem that the most appropriate framework in which to address the evolutionary stability of alternative strategies in salmonids is the theoretical and empirical constructs encompassed by norms of reaction. In other words, are these alternative strategies maintained by adaptive phenotypic plasticity (Warner 1991)? Conceptually, this approach is no different than treating alternative mating strategies as conditional strategies, *sensu* Levins (1968). To incorporate both their environmental and genetic determinants, alternative strategies in salmonids have been modeled as threshold traits (Myers and Hutchings 1986; Hazel et al. 1990; Hutchings and Myers 1994; Hutchings 2002). In the quantitative genetic sense, threshold traits describe characters that are determined by alleles at multiple loci and that can be assigned to one of two or more distinct classes (Roff 1998). The loci affecting threshold traits are assumed to each have some small effect on a trait that varies continuously. For alternative strategies in salmonids, the continuously varying trait may be the concentration of a hormone, amount of lipid deposition, or metabolic efficiency (Thorpe 1986; Metcalfe 1998). Genotypes expressing less than the threshold value of this underlying trait will express one phenotype, while those exceeding the threshold will express the alternative phenotype. It has long been hypothesized that adoption of either the parr or the anadromous strategy in salmonids depends on whether an individual's growth rate in early life exceeds that specified by a growth-rate threshold, that is, that the strategies are conditional upon an individual's state (Leonardsson and Lundberg 1986; Thorpe 1986; Bohlin et al. 1990; Hutchings and Myers 1994). The hypothesis that alternative reproductive strategies may represent conditional strategies, originally developed in the study of salmonids, has since been extended to other groups of organisms (Gross 1996; Gross and Repka 1998).

Growth-rate thresholds can be modeled as norms of reaction for age at maturity. The existence of substantive differences in the incidence of parr maturity among families reared in a common environment (Figure 5.5A) suggests that differences in reaction norms for the probability of parr maturity exist among

individuals in the same population. In their assessment of the utility of artificially selecting against parr maturity, Myers and Hutchings (1986) suggested that alternative mating strategies in Atlantic salmon could be modeled as quantitative genetic threshold traits, whereby the proportion p whose condition or status falls above the threshold adopts one strategy, and the remainder of the population $(1 - p)$ adopts the alternative strategy. As part of their study of alternative strategies in coho salmon, Hazel et al. (1990) adopted a reaction norm approach, depicting norms of reaction for age at maturity as a series of step functions varying among genotypes within a single population (Figure 5.5B).

Using age-specific survival data from the field (Myers 1984) and strategy-specific fertilization data from the laboratory (Hutchings and Myers 1988), Hutchings and Myers (1994) estimated the fitness associated with Atlantic salmon parr and anadromous male strategies as functions of mate competition and age at maturity. Although competition had been an integral part of previous treatments of this subject (e.g., Gross 1985; Myers 1986), Hutchings and Myers (1994) were also able to account for within-strategy differences in age at maturity, an inevitable consequence of environmental variation in growth rate and the influence that growth has on age at maturity. Given the existence of multiple age-specific sets of fitness functions for each strategy, they suggested that the fitnesses of alternative strategies were best represented as multidimensional surfaces. This is because phenotypic plasticity in age at maturity, caused by environmental heterogeneity in the prospects for individual growth, is associated with age-specific differences in the fitness consequences of adopting a given strategy. The points of interaction of these surfaces would then identify an evolutionarily stable continuum of strategy frequencies along which the fitnesses associated with each strategy are equal.

Two predictions from this model relevant to the study of alternative life histories are that: (1) the average fitness of individuals adopting the parr and anadromous strategies is not equal (Figures 2 and 3 in Hutchings and Myers 1994) and (2) selection maintains the frequencies of genes for anadromous male and mature male parr growth rate thresholds in an evolutionarily stable state, rather than the strategies themselves. Subsequent analyses of conditional strategies have drawn similar conclusions (Gross 1996; Gross and Repka 1998).

By adopting a reaction norm approach to the study of alternative life histories, Hazel et al. (1990) and Hutchings and Myers (1994) provide a mechanism by which alternative mating strategies, determined by both genetic and environmental factors, can evolve in variable environments (see also Thorpe et al. 1998). Based on this body of work, growth rate thresholds for parr maturity should differ among populations. This prediction can be represented graphically as a series of population-level reaction norms for each of several populations (Figure 5.5C), which reflect the high degree of variation in the incidence of parr maturity among populations (Myers et al. 1986). The only available data of this type (Little Codroy River, Newfoundland; Myers et al. 1986) do fit a normal cumulative density function (Figure 5.5D), providing the only empirical support to date of the existence of parr maturation threshold reaction norms within natural populations.

2.3. Natural Selection of Reaction Norms in the Wild

The existence of genetic variation in the shapes of reaction norms raises the possibility that the plastic responses of individuals to environmental change can be under selection. Evidence that the shapes of reaction norms are heritable, and can respond to selection, has been revealed by laboratory experiments on *Drosophila* and plants (Schlichting and Pigliucci 1998; Pigliucci 2001a,b). Nonetheless, evidence of such selection in the wild is limited at best. One exception to this may be recently completed research on plasticity in grayling. This work will be described in some detail as it provides some of the best and most compelling evidence for selection on reaction norms in wild populations. Furthermore, if natural selection can act on reaction norms, it is possible that selection induced by anthropogenic activities, e.g., fishing, also may be important. Evidence of plastic changes to life history induced by fishing, and resulting changes to the shapes of reaction norms, will also be discussed below.

The adaptive significance of interpopulation differences in plasticity in salmonids, and the possibility that selection is responsible for these differences, has recently been examined for five Norwegian populations of grayling (Haugen 2000a,b,c; Haugen and Vøllestad 2000). Since their introduction from Lesjaskogsvatn into Hårrtjønn and Øvre Mærrabottvatn in 1910, grayling have dispersed among several other lakes in south-central Norway, including Aursjøen and Osbumagasinet. Over a period of time ranging from 9 to 22 grayling generations, there has been considerable divergence in life history among these populations, notably with respect to age at maturity, size at maturity, and fecundity (Haugen 2000a,b,c).

Population differences in life history have also manifested themselves as differences in the shapes of reaction norms for age and size at maturity (Figure 5.6A; Haugen 2000b). Delayed age at maturity is associated with smaller size at maturity for grayling in four populations, with the population-level reaction norms crossing in state space. Interestingly, and as discussed earlier, the reaction norm for grayling in Øvre Mærrabottvatn expresses an invariance in age at maturity, all individuals maturing at age 3. Consistent with the explanation discussed earlier for population differences in reaction norms for age at maturity in Newfoundland brook charr (Figure 5.4C), there appears to be a direct association between the steepness of the grayling reaction norms and average adult mortality (Haugen 2000b). For individuals aged 4 through 8 years, the instantaneous rate of mortality, Z , was highest (0.77) for Øvre Mærrabottvatn grayling, those apparently favored to reproduce as early in life as possible. By contrast, the reaction norms with the shallowest slopes, encompassing the greatest ranges of ages, are those for Hårrtjønn and Aursjøen grayling, which have the lowest rates of mortality ($Z = 0.36$ for both).

To test the hypothesis that population differences in reaction norms are a result of selection, acting over a comparatively short period of time (9 to 22 generations), Haugen and Vøllestad (2000) undertook a common-garden experiment in which they reared grayling from three different populations under the same experimental conditions in the laboratory. Specifically, they measured

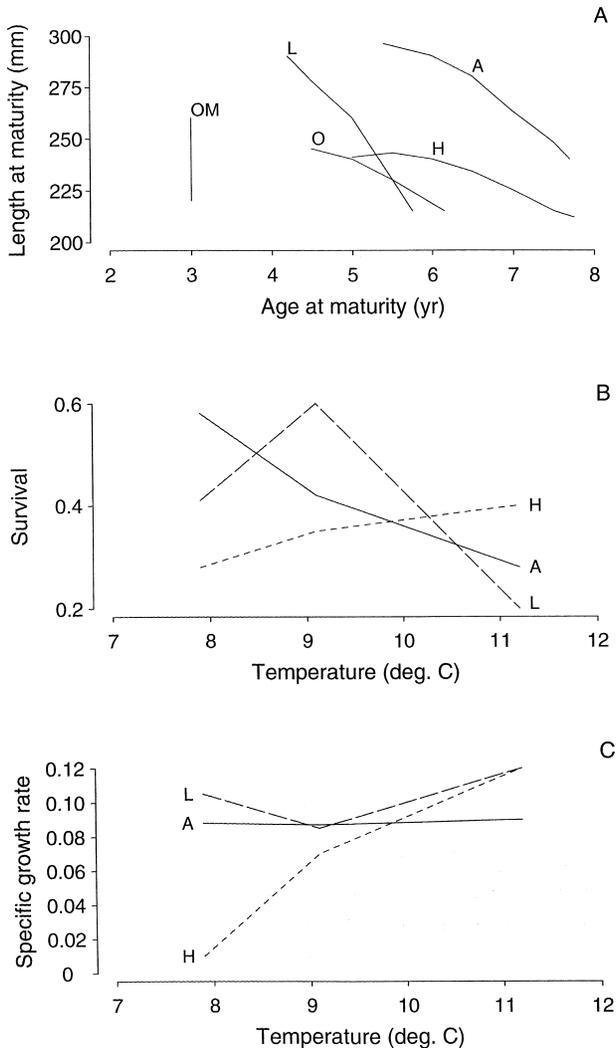


Figure 5.6. Norms of reaction for life history traits in grayling from five populations in south-central Norway. (A) Reaction norms for age and size at maturity for grayling in Øvre Mærrabottvatn (OM), Lesjaskogsvatn (L), Osbumagasinet (O), Hårrtjønn (H), and Aursjøen (A); redrawn from Haugen (2000b). Temperature-based reaction norms for grayling survival (B) and specific growth rate (C) during the first 180 degree-days of exogenous feeding; data are from Haugen and Vøllestad (2000).

survival and specific growth rate during the first 180 degree-days of exogenous feeding at three different temperatures. These temperatures corresponded to the average temperatures experienced by grayling in each of the three populations during this stage of life in the wild: 7.9°C (Aursjøen), 9.1°C (Lesjaskogsvatn), and 11.2°C (Hårrtjønn).

The common-garden experiments revealed significant genetic differences in reaction norms for survival and growth rate among populations. Survival declined with increasing temperature for the “cold” population (Aursjøen), peaked at the intermediate temperature for the “medium” population (Lesjaskogsvatn), and increased with increasing temperature for the “warm” population (Hårrtjønn) (Figure 5.6B). Thus, survival was highest at the temperatures typically experienced by these grayling in the wild. There were also clear differences in plasticity for growth rate among populations (Figure 5.6C), although the fastest growth rates were not always achieved at the temperatures experienced by grayling in the wild (given the existence of life history tradeoffs, this need not be unexpected).

Thus, life history research on grayling has revealed genetic differences in reaction norms for life history traits among populations, providing data consistent with the hypothesis that the shapes of at least some reaction norms (temperature-dependent survival in early life) are adaptive and are the product of natural selection (see also the work by Hendry et al. (1998) on sockeye salmon). The results are also in agreement with research indicating that natural selection can take place over relatively short (10 to 20 generations) periods of time (Hendry and Kinnison 1999; Kinnison and Hendry 2001, 2003—*this volume*).

2.4. Anthropogenic Selection of Reaction Norms

The potential for fishing to cause significant evolutionary change within a population is no different than other forms of predator-induced mortality. Given that differential mortality among genotypes provides the basis for evolutionary change, fisheries can be accurately described as large-scale experiments on life history evolution (Rijnsdorp 1993).

While the potential for genetic change caused by fishing has been acknowledged by comparatively few fisheries scientists (for recent discussions, see Conover 2000; Hutchings 2000; Stokes and Law 2000), the idea that exploitation can cause significant phenotypic changes is widely accepted. Reductions in age at maturity, for example, are one of the best examples of phenotypic change associated with fishing (Policansky 1993). Life history changes often arise because of decreased competition for food and space, increased growth rate resulting from relaxed intraspecific competition, and the negative association that often exists between growth rate and age at maturity (Trippel 1995). Long-term changes in size at maturity have been interpreted as genetic responses to the size-selectivity of fishing gear, for example lake whitefish, *Coregonus clupeaformis* (Handford et al. 1977), pink and chinook salmon (Ricker 1981), Atlantic salmon (Bielak and Power 1986), and European grayling (Haugen and Vøllestad 2001). Recent selection experiments that mimic fisheries and theoretical analyses have also shown that genetic changes in life history are to be expected (Conover and Munch 2002; Hard 2003—*this volume*).

The question of whether fishing can change the shapes of reaction norms by selection has received comparatively little attention. Reznick (1993) hypothesized that the primary effect might be to change the elevation of the reaction

norms, assuming that fishing would select against individuals genetically predisposed to mature at large body sizes. Considering how fishing might affect the slopes of reaction norms, Hutchings (1993b, 1997, 2002) used age-specific survival and fecundity data on brook charr populations to predict how reaction norms for age, size, and reproductive effort at maturity might change in response to increases in adult mortality. As fishing mortality increased, selection was predicted to favor a flattening of reaction norms, notably for age and effort at maturity, such that individuals would be favored to reproduce as early in life as possible and to expend the maximum amount of reproductive effort at that age, irrespective of growth rate.

These hypothesized changes in plasticity resulting from fishing are consistent with the differences in life history reaction norms observed among salmonid populations, such as those described earlier for brook charr (Figure 5.4) and grayling (Figure 5.6). That is, a flattening of the reaction norm for age at maturity (Figures 5.4c, 5.6A) is expected to occur as the probability of realizing the fitness benefits of delayed maturity decline with increases in mortality due to fishing. Similarly, as longevity declines with increased fishing pressure, selection should favor increases in reproductive effort.

It seems reasonable to conclude that fishing can result in selective changes to reaction norms in heavily exploited populations (Hutchings 2002). These changes may involve both the slopes and the elevations of reaction norms for several life history traits. Detecting such changes, however, will be exceedingly difficult, given the near-absence of research on phenotypic plasticity and reaction norms on commercially exploited fishes.

3. Conclusions and Extensions

The evolution of adaptive phenotypic plasticity depends on the existence of additive genetic variation in the shapes of reaction norms (Schlichting and Pigliucci 1998), the sign, magnitude, and temporal constancy of genetic covariances among traits (Turelli 1988; Charlesworth 1990), and the persistence of environmental variation (Via and Lande 1985; Stearns and Koella 1986). Life history traits such as age and size at maturity, egg size, and fecundity are heritable in salmonid fish (Gjedrem 1983; Thorpe et al. 1984; Gjerde 1984a, 1986; Robison and Luempert 1984; Kinnison et al. 2001), so it is not unreasonable to predict that heritable norms of reaction for life history traits exist in this family. Indeed, family-level differences in reaction norms (Beacham and Murray 1985; Haugen 2000c) and genetic differences in population-level reaction norms (Haugen and Vøllestad 2000; B. Jonsson et al. 2001b) suggest that selection on reaction norms in salmonids is inevitable.

To what degree has research on salmonid reaction norms informed us about the evolution of adaptive phenotypic plasticity? Studies of natural populations of brook charr and grayling reveal that the average life history response by individuals to environmental change can differ significantly from one population to the next. This variability will almost certainly affect the ability of populations, and of

individuals within those populations, to adapt to environmental change. Population variation in the shapes of reaction norms for age and size at maturity also suggests conditions under which a form of trait canalization might take place. As adult mortality increases, plasticity is predicted to decline, leading to a relatively invariant phenotypic response across an environmental gradient. Models incorporating genetic and environmental determinants of alternative mating strategies in salmonids illustrate how threshold reaction norms can be applied to the study of conditional strategies influenced by both genetic and environmental factors. And common-garden experiments in salmonids provide evidence of adaptive phenotypic plasticity in the wild and of comparatively rapid responses in the shapes of reaction norms to selection, suggesting that genetic variation in plasticity can be both substantial and heritable in natural populations.

A comprehensive understanding of how genotypes respond to environmental change is fundamental to the study of evolutionary ecology. Recognition of this precept has underpinned the increasingly sophisticated research on reaction norms in the past two decades (Schlichting and Pigliucci 1998; Pigliucci 2001b). This work, embodied in several respects by the salmonid studies discussed here, has laid the foundation for future research initiatives and the questions that they might address:

1. How variable is plasticity among individuals within populations, among populations within species, and among species within and among clades?
2. To what extent do families within populations differ in their average response to environmental change? Is there genetic variation in the shapes of reaction norms within populations?
3. What is the additive component of this genetic variability? To what degree are the shapes of reaction norms heritable?
4. What constrains evolutionary changes in plasticity?
5. How does individual fitness and, by extension, rate of population growth change as phenotypes shift along norms of reaction?
6. How rapidly do reaction norms respond to natural and anthropogenic selection?

Among salmonids, most of the research on plasticity to date has been undertaken within the context of the first question, although relatively little work has been devoted to actually constructing population-level norms of reaction; this is particularly true of traits not directly related to fitness. From a general perspective, the fifth question, arguably the most important of all, has received remarkably little attention in studies of adaptive phenotypic plasticity for *any* organism. If one peruses the most recent reviews of reaction norms (Schlichting and Pigliucci 1998; Mazer and Damuth 2001; Pigliucci 2001a,b), for example, there is little or no discussion of how fitness changes along either individual or family-level norms of reaction.

These questions can be profitably addressed under controlled common-garden and quantitative genetic experiments in the laboratory. However, future research initiatives need also be mindful of the need to rectify the comparative

dearth of plasticity studies that have been conducted under ecologically realistic conditions. Despite the difficulty in establishing appropriate experimental controls in the wild, particularly for many animals, the limited research that has been conducted on salmonids under such conditions suggests that the benefits of such research can be considerable.

Acknowledgments The research was supported by a NSERC (Canada) Research Grant. I thank Andrew Hendry and Steve Stearns for the opportunity to undertake this work. Two anonymous referees provided very helpful comments on an earlier draft of the manuscript.