

REVIEW

Old wine in new bottles: reaction norms in salmonid fishes

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Genetic variability in reaction norms reflects differences in the ability of individuals, populations and ultimately species to respond to environmental change. By increasing our understanding of how genotype \times environment interactions influence evolution, studies of genetic variation in phenotypic plasticity serve to refine our capacity to predict how populations will respond to natural and anthropogenic environmental variability, including climate change. Given the extraordinary variability in morphology, behaviour and life history in salmonids, one might anticipate the research milieu on reaction norms in these fishes to be empirically rich and intellectually engaging. Here, I undertake a review of genetic variability in continuous and discontinuous (threshold) norms of reaction in salmonid fishes, as determined primarily (but not exclusively) by common-garden experiments. Although in its infancy from a numerical publication

perspective, there is taxonomically broad evidence of genetic differentiation in continuous, threshold and bivariate reaction norms among individuals, families and populations (including inter-population hybrids and backcrosses) for traits as divergent as embryonic development, age and size at maturity, and gene expression. There is compelling inferential evidence that plasticity is heritable and that population differences in reaction norms can reflect adaptive responses, by natural selection, to local environments. As a stimulus for future work, a series of 20 research questions are identified that focus on reaction-norm variability, selection, costs and constraints, demographic and conservation consequences, and genetic markers and correlates of phenotypic plasticity.

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Introduction

‘One must constantly keep in mind the elementary consideration which is all too frequently lost sight of in the writings of some biologists; what is inherited in a living being is not this or that morphological character, but a definite norm of reaction to environmental stimuli. [A] mutation changes the norm of reaction.’

Dobzhansky (1937)

Among the fundamentals of evolutionary biology is the stipulation that the phenotypic variability expressed by any trait is a function of the genetic variability in that trait (additive, epistatic and dominance variation), variability caused by the environment and variability resulting from the way in which the genetic variability interacts with the environmental variability. It was the third of these sources to which Dobzhansky (1937) focussed attention in the quote cited above from *Genetics and the Origin of Species*. Here, one of the great thinkers of evolutionary biology encapsulated what he perceived to be an overlooked yet fundamentally important element

of evolutionary change, namely the ways in which mutation and selection act upon heritable variability in an individual’s norm of reaction.

Richard Woltereck introduced the term *Reaktionsnorm* over a century ago, justifying Blackburn and Schneider’s (1994) characterisation of the subject matter as ‘old wine’ in their well-articulated description of the support by Dobzhansky, and others, of evolutionary research on plasticity. Woltereck (1909) focussed on exploring how the height of the head (as a percentage of body length) in different clones of *Daphnia* and *Hyalodaphnia* varied as a function of the amount of available food (algae). Norms of reaction can be described heuristically as linear or nonlinear functions that characterise the pattern with which the phenotypic value of a trait, for a given genotype, changes with the environment. Reaction norms provide graphical representations of phenotypic plasticity—the ability of a genotype to produce different phenotypes across an environmental gradient (Schlichting and Pigliucci, 1998; Sultan and Stearns, 2005); in effect, they describe how individuals respond to environmental change. As such, by providing information about the magnitude of trait plasticity and the presence of genotype \times environment interactions on the phenotypic expression of a given trait (de Jong, 2005), norms of reaction have great potential to increase our understanding of the ability of genotypes, and ultimately populations and species, to respond adaptively to natural and human-induced environmental variability, including climate change (Visser, 2008).

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Overlooked during the year of the bicentenary of the birth of Charles Darwin, and the sesquicentennial of the publication of *On the Origin of Species*, was the centenary anniversary of the first publication on reaction norms (Woltereck, 1909). As Schlichting and Pigliucci (1998) noted, the history of research on phenotypic plasticity and reaction norms is a lengthy one, beginning perhaps with Baldwin's 'new factor in evolution': individuals differ not only in phenotype, but also in the way that the phenotype can be altered by changing environmental circumstances (Baldwin, 1896). Johanssen (1911), writing that Woltereck's *Reaktionsnorm* were 'fully compatible with the genotype-conception', linked reaction norms with genotypes and clearly recognised their potential importance in evolution.

It is not surprising, then, to discover a wealth of historical and contemporary research on phenotypic plasticity and reaction norms in many species, particularly plants, given their propensity for producing highly variable phenotypes (Goldschmidt, 1940; Schmalhausen, 1949; Bradshaw, 1965; Latta *et al.*, 2007). Given the extraordinary variability in morphology, behaviour and life history in salmonids (for example, Klemetsen *et al.*, 2003; Hendry and Stearns, 2004), one might anticipate the research milieu on reaction norms in these fishes to be empirically rich and intellectually engaging. This provides one impetus for this review of reaction norm research in salmonid fishes. Secondary objectives include opportunities to identify means by which plasticity research on salmonids has informed, and can inform, research on evolutionary change (cf. Hendry and Stearns, 2004), and to identify questions and predictions that might stimulate future research.

For clarification, in this review I am implicitly assuming the slope of a trait's reaction norm (that is, its plasticity) to be a heritable trait in and of itself upon which selection can act (Via *et al.*, 1995). An alternative view (the 'character-state' approach) asserts that, rather than being a target of selection, plasticity evolves as a by-product of selection on different values of the same trait in different environments (Via and Lande, 1985; Via *et al.*, 1995). De Jong (1995) argued that the 'reaction-norm' model was more appropriate when studying graded responses to continuous environments (arguably more relevant to species such as salmonids), whereas the character-state model may be more appropriate when studying discrete responses to discrete environments. Notwithstanding the debate as to which theoretical model is more generally applicable (for example, Via *et al.*, 1995), the assumption that selection can act on reaction-norm slopes is supported by experimental work (for example, Scheiner, 2002; Nussey *et al.*, 2005) and underlies recent evolutionary models of how plasticity affects adaptation to novel environments (Lande, 2009; Chevin *et al.*, 2010). In addition, I am assuming, following Lande (2009), that both the slopes and the elevations of reaction norms can be genetically variable.

On another point of clarification, this review includes reaction norms for survival, in addition to those traits that might be more typically thought of as being plastic (for example, morphological, meristic, life history, behavioural and physiological traits). Although the construction of survival reaction norms might not initially seem intuitive, they have been examined in a variety of species (as this review will illustrate) and there

is no strikingly compelling reason to exclude them. Quantitative geneticists, for example, have long considered survival to represent a heritable trait upon which selection can act (for example, Falconer, 1960; Bradford, 1969; Johnson *et al.*, 1999). And although survival represents a manifestation of the actions of multiple genes and traits acting singly and in concert, in response to environmental change, the same is true for most traits for which plasticity has been estimated, such as body size, growth rate, swimming speed and foraging efficiency. Indeed, one could make the argument that, because of its typically high association with fitness, reaction norms for survival provide better representations of potential adaptation than reaction norms for single traits.

Trends in research on salmonids

Phenotypic plasticity

To quantify temporal changes in research on plasticity and reaction norms, I searched the ISI Web of Science, using various combinations of keywords. To obtain papers on phenotypic plasticity and reaction norms in all species, the searches were restricted to the keyword combinations of 'phenotypic' and 'plasticity', and 'reaction' and 'norm', respectively. To obtain papers on plasticity and reaction norms undertaken on salmonids only, I used the above combinations in conjunction with the following: *Salmo*, *Salvelinus*, *Oncorhynchus*, *Coregonus*, *Thymallus*, salmon, trout, char, charr, whitefish and grayling. As articulated further below, it must be acknowledged that literature searches such as those employed here cannot be taken to represent the absolute number of papers published on a particular subject matter. Nor can one assume that the earliest papers identified by these searches truly represent the 'first' papers on either phenotypic plasticity or reaction norms; they almost certainly do not. However, notwithstanding these caveats, literature searches such as those undertaken here should reasonably reflect temporal trends in research in these subject areas, and that is the primary purpose for presenting these analyses here.

Over the past 50 years, the number of papers on phenotypic plasticity was remarkably few until 1990, whereafter they increased dramatically (Figure 1a). Since the publication of fewer than five papers (all on plants) in the 1960s (for example, Bradshaw, 1965; Basak and Chaudhuri, 1967), 12 in the 1970s and 69 in the 1980s, the number of papers on plasticity across taxa increased to 1567 in the 1990s and to 4419 from 2000 to 2009 (a 282% decadal increase). By comparison, according to the ISI search protocol employed here, there were no papers on phenotypic plasticity in salmonids until 1991; 50 papers were published in the 1990s and 180 from 2000 to 2009 (a 360% increase). So, despite the slower start, the number of papers on plasticity in salmonids appears to be increasing at a somewhat faster rate at present, on a decadal scale, than those on other taxa.

Although simple keyword searches can reveal qualitatively interesting temporal patterns, there are limitations associated with such an approach, which can bias the results both negatively and positively. In this context, all relevant papers may not have been secured because some authors might have neglected to include 'pheno-

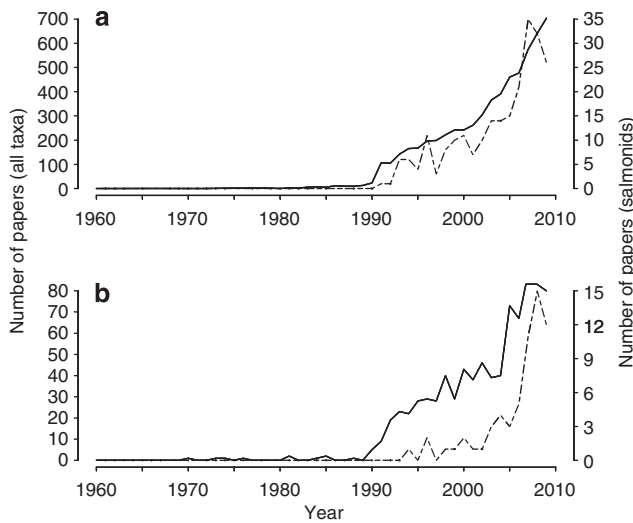


Figure 1 Temporal trends in publications on (a) phenotypic plasticity and (b) reaction norms for all taxa (solid lines) and for salmonid fishes (dashed lines).

typic plasticity' either in their title or among their keywords. On the other hand, authors' selection of keywords can introduce a positive bias. For example, the earliest paper identified here on phenotypic plasticity in salmonids is a one-page introduction (which has never been cited, until now) to a special issue in *Ecology* (Gordon and Matson, 1991); the keywords were those identified by the organisers of the special issue, rather than necessarily being reflective of the issue's contents (none of the papers in the special issue were identified in the keyword search). As an additional positive bias, the keyword search protocol as applied to salmonid fishes unhelpfully identified papers on plasticity research on taxa other than salmonids, again because of the authors' selection of keywords.

The earliest papers in the ISI database that met the keyword criteria identified above, and that truly involved research on plasticity on a salmonid, were meristic and morphometric studies undertaken on lake herring, *Coregonus artedii* (Shields and Underhill, 1993), and research on behavioural and life-history plasticity on Atlantic salmon, *Salmo salar* (Metcalfe, 1993; Hutchings, 1993a). This work was followed in 1994 by behavioural and life-history studies on brook trout, *Salvelinus fontinalis* (McLaughlin and Grant, 1994), and Atlantic salmon (Hutchings and Myers, 1994), and on resource polymorphisms in a number of fishes, including salmonids (Robinson and Wilson, 1994).

Notwithstanding the methodological caveats, there is reason to believe that the dearth of salmonid plasticity papers before and during the early 1990s revealed by the ISI keyword search is an accurate reflection of the state of plasticity research on these fishes, particularly within an evolutionary context, at that time. Blackburn and Schneider (1994), who argued in effect that the study of genotype \times environment interactions across taxa was an emerging, albeit overdue, trend in evolutionary biology, made mention of only two papers on salmonid plasticity (Stickland *et al.*, 1988; Eskelinen, 1989) among their 74 citations. Neither Stearns and Koella (1986), Stearns (1989) nor Reznick (1993) cited papers on salmonid

plasticity (save for those supporting the long-standing observation that age at maturity declines with individual growth rate; Alm, 1959). Without being unduly semantic, for the purpose of this review, it is helpful to distinguish studies for which the research objective was to focus on plasticity *per se* from an ecological or evolutionary perspective from studies that simply revealed evidence of plasticity as an indirect consequence of the primary purpose for which the work was undertaken. In this regard, it seems fair to conclude that studies on the evolutionary ecology of salmonid plasticity were uncommon before the early 1990s.

Reaction norms

Although the number of publications on phenotypic plasticity in salmonids ($n=260$)—a family containing more than 150 species (Nelson, 2006)—pales by comparison with those published on some genera (for example, 542 papers on plasticity in the ISI database on *Drosophila* spp. through 2009), it dwarfs the number of papers on salmonid reaction norms ($n=62$ through 2009). Contrary to the steady increase in papers on reaction norms across all taxa through the 1990s, there was a surprising, almost decadal, time lag in the onset of a similar increase in papers on reaction norms in salmonid fishes (Figure 1b). On the basis of the output of the ISI keyword search, publications in which researchers had directed their research on salmonid reaction norms before 2000 were those undertaken on Atlantic salmon (Hutchings and Myers, 1994; Hutchings and Jones, 1998), brown trout, *Salmo trutta* (Andreeva *et al.*, 1996; Einum and Fleming, 1999) and brook trout, *Salvelinus fontinalis*, (Hutchings, 1996), although the 'reaction norms' described by Einum and Fleming (1999) actually depicted responses within, rather than between, genotypes.

As mentioned previously, limitations of the keyword-search approach mean that some publications that had specifically focussed on reaction norms in salmonids were missed. These include the threshold reaction norms for alternative reproductive tactics hypothesised by Hazel *et al.* (1990), for which one example was that of coho salmon, *Oncorhynchus kisutch*, and the empirically based reaction norms for age, size and reproductive effort at maturity (and how they might change under fisheries-induced evolution) constructed by Hutchings (1993b). Although excluded from the keyword search results, there were salmonid reaction norms published before 1990; however, they were not described as such. With rare exception (for example, Beacham, 1988), the primary focus of these studies was not genotype \times environment interactions or genetic differentiation in plasticity. Rather, the objective of much of this work was to compare the 'developmental performance' of individuals from different families and different populations under variable hatchery incubation environments (usually different rearing temperatures). With this in mind, there is a least one body of work, by Terry Beacham and Clyde Murray (and there may be others in the hatchery/aquaculture literature), that provides a wealth of information on genotype \times environment interactions for characteristics in early life (typically during the embryonic or immediate post-hatching stages) among families, occasionally populations, in salmonids (for example, Beacham and Murray, 1985, 1986a,b, 1989, 1990).

Genetic variability in continuous reaction norms

Common-garden experiments

One of the strongest means of determining whether phenotypic differences between groups are genetically based is to undertake controlled experiments that minimise or negate the influence of environmental variation on the trait(s) of interest. This review of genetic differentiation in salmonid reaction norms focusses on those studies that employed a common-garden experimental protocol or some appropriate variant thereof (for example, reciprocal transplant experiment).

Including papers that fulfilled the keyword search criteria for salmonid reaction norms through 2009 ($n = 62$) and the eight 'reaction-norm' papers published by Beacham and Murray, fewer than 25 provide experimental evidence of genetic variability in reaction norms among members of the same species (Table 1; Peres-Neto and Magnan (2004) constructed reaction norms at the species level). Most of these are for univariate continuous reaction norms, that is, those for which the phenotypic value of a single trait changes continuously with changes to the environment, as opposed to univariate traits that vary with the environment in a discontinuous manner. The former will be discussed here, and the latter, which will include threshold and bivariate reaction norms, will be discussed in the following section.

Differences among families

Published studies of genetic variability in salmonid reaction norms at the family level appear to be limited to Pacific salmon. The largest compendium of work on genotype \times environment interactions at the family level in salmonids is that completed by Beacham and Murray. Their research, which encompassed all North American species of the genus *Oncorhynchus*, except *O. mykiss* and *O. clarki*, documented significant genotypic differences in responses by several traits expressed in early life to changes in water temperature. Their earliest work revealed highly variable slopes in norms of reaction for survival and somewhat less variability in those for length at emergence in chum salmon, *O. keta* (Beacham and Murray, 1985; Figure 2), a pattern that appeared to hold true for pink salmon, *O. gorbuscha*, when reared at the same three temperatures (4, 8 and 12 °C; Beacham and Murray, 1986a). Perhaps, because of an expansion of the temperature range in later studies of sockeye, *O. nerka* (2, 4, 8, 12 and 15 °C; Beacham and Murray, 1989) and coho salmon (1.5, 2, 4, 8 and 12 °C; Murray *et al.*, 1990), higher family-level variability in reaction-norm slope and elevation, than that documented previously for pink and chum salmon, becomes evident in reaction norms for egg survival and body size. Family-level differences have also been documented for developmental time to hatching in both sockeye and Chinook salmon (Beacham and Murray, 1989), with Kinnison *et al.* (1998) noting that families of New Zealand Chinook salmon that developed relatively rapidly at warm temperatures did not also develop rapidly at colder temperatures.

A reciprocal transplant experiment recently revealed genetic differences in early-life reaction norms at the family level in Chinook salmon, *O. tshawytscha*. Comparing families from Big Qualicum and Quinsam Rivers in

British Columbia (Canada), Evans *et al.* (2010) reported differences in the slopes of reaction norms for survival at two developmental stages and for length in early life. Interestingly, they found survival reaction norms to have lower variability during the yolk-sac stage (Figures 3a and b) than during the later fry stage when exogenous feeding begins (Figures 3c and d); genotype \times environment interactions for fry length appeared to be similar to those for survival during the fry stage (Figures 3e and f).

Although the number of species examined to date has been comparatively few, it seems reasonable to conclude that there can be substantial genetic variability at the family level in salmonid reaction norms for survival and body size in early life.

Differences among population crosses

The level of genetic differentiation between population crosses, such as F1 hybrids or backcrosses, appears to exceed that between families within the same population (or cross). On the basis of the ISI literature search, four studies have employed a population-cross comparison to study genetic variability in plastic responses by salmonids to environmental change. Three will be discussed here and the fourth (Piché *et al.*, 2008) later in the section on discontinuous reaction norms.

The first of these studies examined compensatory growth in Atlantic salmon. Fraser *et al.* (2007) crossed Nova Scotian (Canada) salmon from Stewiacke River with those from LaHave River and then compared growth trajectories during and following a period of food deprivation. Their objective was to determine whether the accelerated, or compensatory, growth that typically follows periods of environmentally induced growth depression differed between Stewiacke \times Stewiacke salmon, LaHave \times LaHave salmon and Stewiacke \times LaHave F1 hybrids.

They predicted that long-distance migrants would express greater efficiencies in growth and maintain higher growth trajectories following food restriction than short-distance migrants. This hypothesis was based on the expectations that long-distance migrants (a) require larger body sizes to offset presumably higher energetic costs of migration and (b) face greater time constraints for growth, given that they must presumably depart from feeding areas at an earlier date than short-distance migrants to return to spawning areas at approximately the same spawning period. Under controlled environmental conditions, they found that the longer-migrating LaHave salmon grew more rapidly and experienced faster compensatory growth than Stewiacke salmon, which tend to migrate relatively short distances from their natal river; growth rates of F1 hybrids were generally intermediate. Their work indicates that compensatory growth rates can differ genetically among population crosses (although this need not always be the case; Morris *et al.*, 2011) and that these differences may be adaptive.

Second-generation backcrosses, one of which involved Stewiacke River salmon, were used to explore the consequences of interbreeding between salmon that escape from aquaculture farms and their wild counterparts. Darwish and Hutchings (2009) compared temperature-based reaction norms for embryonic development, yolk-sac volume, growth, survival and body size among three crosses that involved salmon from Tuskett

Table 1 Research on salmonid fishes in which putative genetic differentiation in reaction norms is hypothesised to exist

Species	Variables	Scale of differentiation	References
<i>Coregonus clupeaformis</i>	PMRN	Temporal	Wang <i>et al.</i> (2008)
<i>Oncorhynchus gorbuscha</i>	Early-life traits; temperature	Family; population; species	Beacham and Murray (1986a, 1990) ^a ; Beacham (1988) ^a
<i>O. keta</i>	Early-life traits; temperature	Family; population; species	Beacham and Murray (1985, 1990) ^a ; Murray and Beacham (1987) ^a ; Beacham (1988) ^a
	Meristics	Life-history morph	Beacham and Murray (1986b) ^a
	PMRN	Temporal	Morita and Fukuwaka (2007); Fukuwaka and Morita (2008)
<i>O. kisutch</i>	Age at maturity; growth, condition	Life-history morph	Hazel <i>et al.</i> (1990); Tomkins and Hazel (2007)
	Early-life traits; temperature	Family; population; species	Murray <i>et al.</i> (1990) ^a ; Beacham and Murray (1990) ^a
<i>O. nerka</i>	Age at migration; growth	Population	Quinn <i>et al.</i> (2009)
	Early-life traits; temperature	Family; population; species	Beacham and Murray (1989, 1990) ^a ; Hendry <i>et al.</i> (1998) ^a
<i>O. tshawytscha</i>	Early-life traits	Family; population	Evans <i>et al.</i> (2010) ^a ; Beacham and Murray (1989) ^a
	Early-life traits; temperature	Family; species	Murray and Beacham (1987) ^a ; Beacham and Murray (1990) ^a ; Kinnison <i>et al.</i> (1998) ^a
<i>Salmo salar</i>	Age at maturity; growth	Life-history morph; population cross; population	Hutchings and Myers (1994); Nicieza <i>et al.</i> (1994) ^a ; Hutchings and Jones (1998); Piché <i>et al.</i> (2008) ^a
	Trypsin; temperature	Individual	Rungruangsak-Torrissen <i>et al.</i> (1998) ^a
	Early survival; pH	Population cross; population	Fraser <i>et al.</i> (2008) ^a
	Several early-life traits; temperature	Population cross	Darwish and Hutchings (2009) ^a
	Size and condition; compensatory growth	Population cross	Fraser <i>et al.</i> (2007) ^a
	PMRN	Temporal	Vainikka <i>et al.</i> (2010)
<i>S. trutta</i>	Lactate dehydrogenase in muscle; temperature	Life-history morph	Andreeva <i>et al.</i> (1996) ^a
	Several early-life traits; temperature	Population	Jensen <i>et al.</i> (2008) ^a
<i>Salvelinus alpinus</i>	Morphology; swimming speed	Species	Peres-Neto and Magnan (2004) ^a
<i>S. fontinalis</i>	Life history traits; growth	Population	Hutchings (1993b, 1996)
	Morphology; swimming speed	Species	Peres-Neto and Magnan (2004) ^a
	Morphology	Life-history morph	Proulx and Magnan (2004) ^a
	Gene transcription and growth; salinity	Individual	Côté <i>et al.</i> (2007) ^a
	PMRN	Temporal	Okamoto <i>et al.</i> (2009)
<i>Thymallus thymallus</i>	Several early-life traits; temperature	Population	Haugen and Vøllestad (2000) ^a
	Survival; age and size at maturity	Population	Haugen (2000) ^a

Abbreviation: PMRN, probabilistic maturation reaction norm.

With the exception of variables identified as PMRN (for age and size at maturity), the scale of genetic differentiation is identified as being: among individuals; between families; between life-history morphs (for example, resident vs migratory, normal vs dwarf, pelagic vs littoral); between population crosses (for example, F1 inter-population hybrids, backcrosses); between populations; or between species. For PMRNs, differentiation is temporal in scale.

^aStudies reporting results from a common-garden experimental protocol.

River (Nova Scotia), Stewiacke River, and a farmed population four generations removed from the wild (Saint John River, New Brunswick, Canada): Tusket × Tusket pure cross; Tusket × (Tusket × Stewiacke) backcross; and Tusket × (Tusket × Farmed) backcross. Reaction norms differed markedly among crosses, indicating that introgression involving individuals with comparatively few genetic differences can change the magnitude of genotype × environment interactions considerably. If plasticity represents an adaptive response to local environments, changes to reaction norms resulting from outbreeding, be it with wild or farmed salmon, are unlikely to have a beneficial influence on fitness, although Darwish and Hutchings (2009) were unable to predict precisely what the consequences of such interbreeding might be for their crosses.

The potential fitness consequences of altered reaction norms resulting from introgression were, however,

examined by Fraser *et al.* (2008) in their work on Atlantic salmon that inhabit acidified and non-acidified rivers in Nova Scotia. They compared the cumulative survival of alevins from six different crosses after 69 days of exposure to one of five different levels of pH (Figure 4). Comparing reaction norms among pure crosses at the highest levels of acidity (pH = 4.6 and 4.9), salmon from the acidified Tusket River (which had experienced acid rain and low pH for 4–5 salmon generations) experienced considerably higher survival than both farmed salmon and wild salmon from the non-acidified Stewiacke River. The reaction norms of Tusket salmon crossed and backcrossed with farmed salmon had lower elevations than that of the pure Tusket cross, whereas that of the F2 Tusket × Farmed cross was surprisingly higher. These differential survival responses to differing levels of pH provide some of the strongest evidence to date of local adaptation in a reaction norm in salmonids.

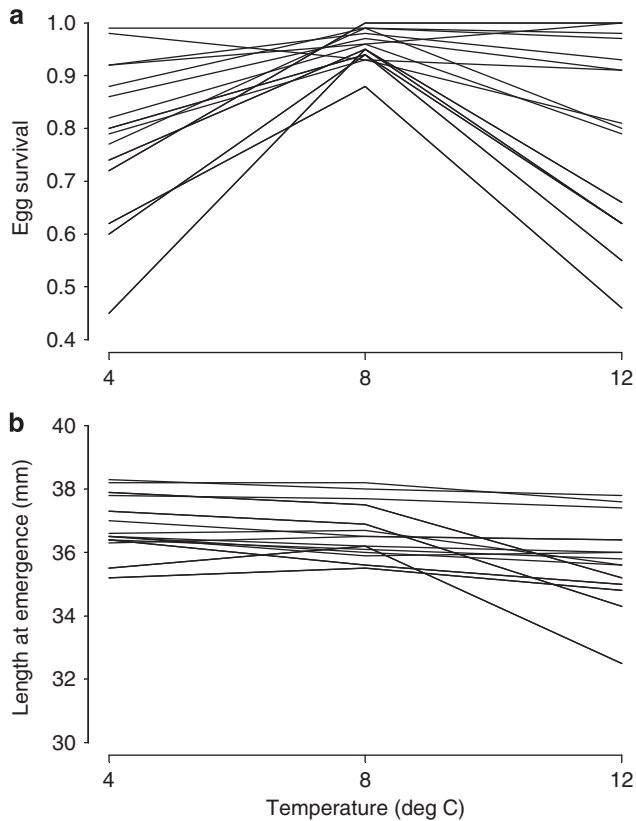


Figure 2 Reaction norms for egg survival and length at emergence for families of chum salmon, *Oncorhynchus keta*, from Nitinat River, British Columbia, Canada. Data re-drawn from Beacham and Murray (1985).

Differences among populations

Among the early common-garden experimental studies to explore the adaptive significance of naturally occurring variability in salmonid reaction norms was that undertaken on several wild populations of European grayling, *Thymallus thymallus*, by Haugen (2000) and Haugen and Vøllestad (2000) in central Norway. Although they once shared a common ancestor, the populations had been reproductively isolated from one another, and exposed to different environments, for a period of 13–18 grayling generations. This period of time was sufficient to allow for population differences to emerge in the responses of several early-life traits to changes in temperature (Figures 5a–f). Highly significant sire and sire \times temperature effects provided additional evidence that the differential responses to temperature had a genetic basis. Given that the grayling populations, because of their common ancestry, must have once expressed the same set of reaction norms, the question was raised as to whether the present-day divergence had been caused by natural selection. Arguments in favour of the hypothesis that population differences in reaction norms represented an adaptive response to local environments were based on observations that the traits examined were closely linked to fitness and that grayling survival was highest at the temperatures that they were most likely to experience in the wild (Figure 5g).

Adaptation to local temperature was also the primary focus of Jensen *et al.*'s (2008) study of four Danish populations of brown trout, *Salmo trutta*. Using a

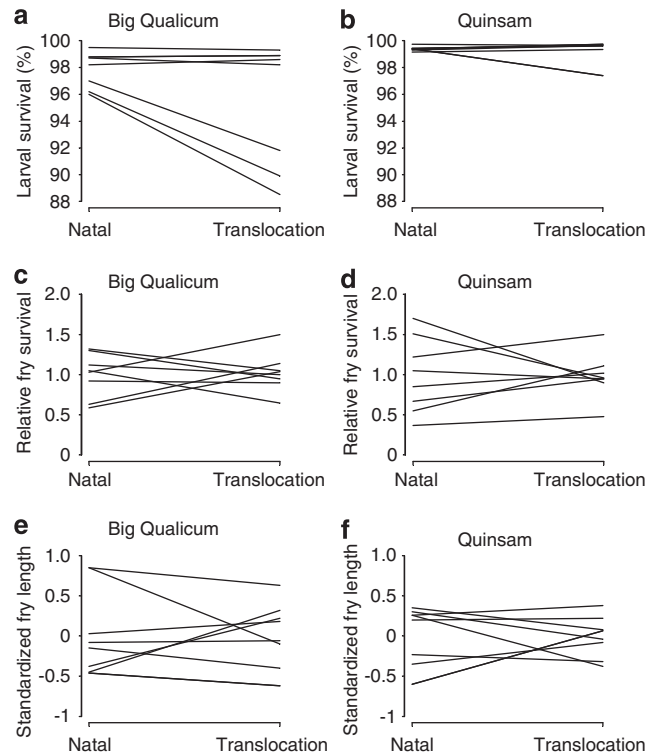


Figure 3 Reaction norms for early life-history traits at the family level for Chinook salmon, *Oncorhynchus tshawytscha*, from Big Qualicum and Quinsam Rivers, British Columbia, Canada: (a) and (b) larval (embryonic) survival; (c) and (d) standardised measures of fry survival; and (e) and (f) standardised measures of fry length. Lines represent reaction norms for each of eight paternal half-sib families reared in a hatchery located either on their natal river or reciprocally transplanted to the hatchery on their non-natal river. Data re-drawn from Evans *et al.* (2010).

common-garden experimental protocol, significant differences were documented in population-level reaction norms for several early life-history traits (Figure 6). Coupled with this variability was the observation that quantitative trait differentiation (Q_{ST}) exceeded neutral molecular differentiation (F_{ST}) for body length at two different developmental stages (alevin, swim-up). As documented by Haugen and Vøllestad (2000) for grayling, Jensen *et al.* (2008) found evidence of genetic variability in plasticity among individuals within populations, as indicated by significant sire \times temperature interactions. They further supported their conclusion that population differences in reaction norms were a consequence of natural selection by arguing for potentially adaptive responses by alevin length and growth rate to temperatures that the populations were most likely to experience in the wild.

Although not focussing on the adaptive significance of population differentiation in plasticity *per se*, other studies have documented mixed evidence for genetic differences in reaction norms. Hendry *et al.* (1998), for example, did find significant population differences in how survival from fertilisation to hatching varied with incubation temperature in sockeye salmon. By contrast, Kinnison *et al.* (1998) did not find population-level differences in reaction norms for early developmental traits in New Zealand Chinook salmon. The latter is an example of a study wherein reaction-norm divergence

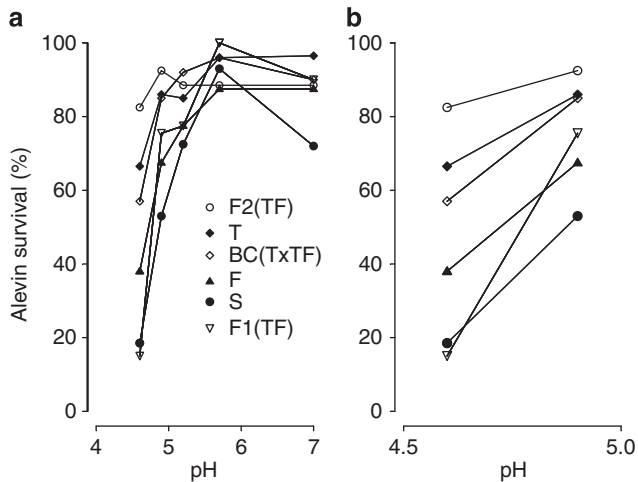


Figure 4 Survival reaction norms of alevins (over a 69-day period) for various cross-types of Atlantic salmon, *Salmo salar*, as a function of pH ranging between (a) 4.6 and 7.0 and between (b) 4.6 and 4.9. Population crosses: Tusket River (acidified; solid diamonds); F = Farmed salmon (non-acidified source; solid triangles); S = Stewiacke River (non-acidified; solid circles); F1(TF) = F₁ Tusket × Farmed hybrids (open, inverted triangles); F2(TF) = F₂ Tusket × Farmed hybrids (open circles); BC(T × TF) = backcross(F₁ TF × T) (open diamonds). Re-drawn from Fraser *et al.* (2008).

was expressly assessed but not found and, thus, not emphasised by the researchers. The degree to which this is common in the salmonid literature is not known.

Among the first examples of a genotype × environment interaction at the level of gene transcription in salmonids is the study undertaken by Côté *et al.* (2007) on brook trout. Using a common-garden experimental protocol, they found levels of mRNA transcription for growth hormone receptor to be significantly higher when trout were reared in salt water than in fresh water (Figure 7). In a similar vein, the expression of major histocompatibility complex genes (for example, major histocompatibility complex class II genes) has been shown to change with temperature in rainbow trout (Nath *et al.*, 2006) and brook trout (Croisetière *et al.*, 2010). A particularly fascinating result reported by Croisetière *et al.* (2010) is that the way in which the expression of the major histocompatibility complex class IIβ gene in brook trout changes with temperature (which is approximately the elevation of the genomic reaction norm) appears to be associated with the base-pair length of an associated temperature-sensitive mini-satellite, which may be suggestive of a genomic underpinning for plasticity. This work is among recent studies to investigate reaction-norm variability at the gene transcription level in fishes (for example, Aubin-Horth and Renn, 2009; Aubin-Horth *et al.*, 2009; McCairns and Bernatchez, 2010).

Genetic variability in discontinuous and bivariate reaction norms

Alternative reproductive tactics

Members of the family Salmonidae have provided well-documented examples of discontinuous variation in life history and behaviour. One of the most phenotypically

extreme examples of alternative life histories in vertebrates is found in Atlantic salmon. Mature male parr reproduce at sizes 2–3 orders of magnitude smaller (by weight) and at much less than half the age of anadromous males, which breed following a migration to sea (Jones, 1959; Hutchings and Myers, 1988; Fleming, 1996). Similarly variable anadromous and non-anadromous alternative phenotypes exist in brown trout (for example, Hindar *et al.*, 1992; Klemetsen *et al.*, 2003) and Chinook salmon (Healey, 1991), whereas members of the genera *Salvelinus* and *Coregonus* are better known for their extraordinary life-history variability in the absence of seaward migrations (for example, Sandlund *et al.*, 1992; Bernatchez *et al.*, 2010). Somewhat less extreme differences in size and age, although no less interesting evolutionarily, characterise differences between large ‘hooknose’ and smaller ‘jack’ males in *Oncorhynchus* spp. (Gross, 1985; Quinn, 2005), both of which migrate to sea before reproduction.

Maturation as one of two alternative reproductive phenotypes (as does the probability of smolting and migrating to sea at a particular age; Thorpe, 1986; Beckman and Dickhoff, 1998; Thorpe *et al.*, 1998) appears to depend on the attainment of a critical growth rate, body size, social dominance status or some combination thereof (Glebe *et al.*, 1978; Leonardsson and Lundberg, 1986; Thorpe, 1986; Metcalfe *et al.*, 1989; Bohlin *et al.*, 1990). To account for the influence of both environmental and genetic influences on the expression of alternative reproductive phenotypes, their incidence has been modelled in the quantitative genetic sense as a threshold trait having an underlying normal distribution for liability, Myers and Hutchings (1986) being the first to do so for salmonids. Threshold traits describe characters determined by alleles at multiple loci that can be assigned to one of two or more distinct classes (Roff, 1996). Individuals whose growth rate, size or condition (heritable traits, albeit heavily influenced by local environmental conditions) exceeds a genetically determined threshold would adopt one phenotype, whereas those whose state fell below the threshold would adopt the alternative phenotype. Application of threshold reaction norms to salmonid life-history research was a logical extension of this theoretical and empirical work.

Threshold reaction norms

The hypothesis that life-history patterns in salmonids are influenced by thresholds of some form is not new. Elson (1957), for example, suggested that Atlantic salmon need to attain a specific body length before they migrate to sea as smolts. Several authors have argued that attainment of a body-size or growth-rate threshold (or some proxy thereof) determines whether Atlantic salmon migrate to sea at a given age or mature as parr in fresh water (Bailey *et al.*, 1980; Leonardsson and Lundberg, 1986; Thorpe, 1986; Bohlin *et al.*, 1990). Thorpe (1986) alluded to genetically determined thresholds when he postulated that the growth rate that preceded a salmon’s life-history decision to migrate to sea or not depended on a regulator of appetite that was itself genetically determined through a regulator of developmental performance.

The first discontinuous patterns of phenotypic variability to be explored explicitly as reaction norms in salmonids (coho salmon) appear to be those constructed

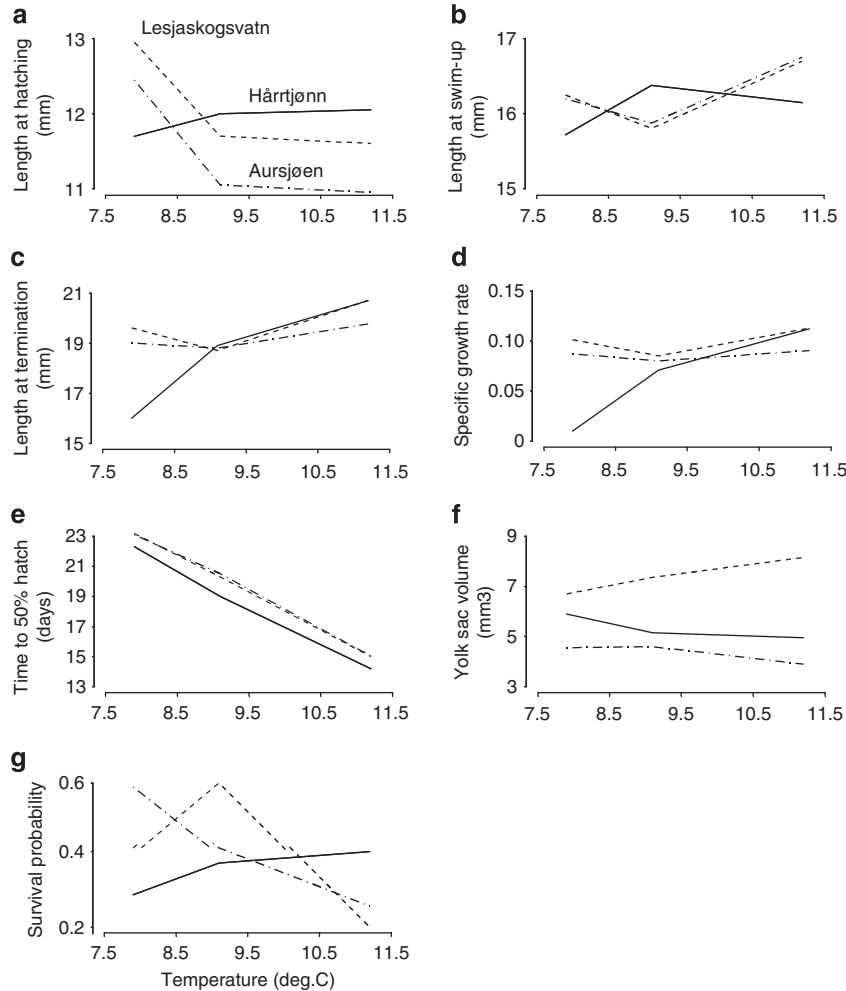


Figure 5 Reaction norms for early life-history traits, as a function of temperature, for grayling, *Thymallus thymallus*, from three populations in central Norway: Aursjøen—cold-water population (dot-dashed lines); Lesjaskogsvatn—intermediate-temperature population (dashed lines); Hårtjønn—warm-water population (solid lines). Variables examined included: (a) length at hatching; (b) length at swim-up; (c) length at experiment termination; (d) specific growth rate; (e) time to 50% hatching; (f) yolk-sac volume; and (g) survival probability. Data re-drawn from Haugen and Vøllestad (2000).

by Hazel *et al.* (1990). They developed a model for the evolution and maintenance of alternative reproductive phenotypes within populations in which they treated conditional strategies as polygenic threshold traits. In effect, they assumed that the reaction norm of each genotype—represented graphically as a step function (Figure 8a)—is characterised by an environmentally triggered threshold, or switch-point, at which the genotype would adopt the alternative maturation phenotype. Framing their argument within the context of evolutionarily stable strategies, Bohlin *et al.* (1990) had also argued that salmonid parr maturity was determined by a genetically determined, environmentally triggered threshold. Independently of Hazel *et al.*'s (1990) research, Hutchings and Myers (1994) adopted a reaction-norm model to account for the evolutionary persistence and stability of alternative maturation phenotypes in Atlantic salmon, arguing that genetic variability in reaction norms within populations should logically lead to genetic variability in parr-maturation thresholds among populations, a prediction also proffered by Bohlin *et al.* (1990) for brown trout and Atlantic salmon.

Although family-level differences in the incidence of parr maturity had been documented previously (for example, Saunders *et al.*, 1982), it was approximately a decade after the threshold reaction-norm papers that field evidence of population differences in parr-maturation thresholds were documented in salmonids: Atlantic salmon in Scotland (Baum *et al.*, 2004) and Québec (Aubin-Horth and Dodson, 2004; Aubin-Horth *et al.*, 2006); and masu salmon, *O. masou*, in Japan (Morita and Nagasawa, 2010). The first experimental evidence of population genetic differentiation in threshold reaction norms in salmonids was provided by Piché *et al.* (2008), based on common-garden experiments undertaken on crosses in Nova Scotia (Figure 8b), although Nieceza *et al.* (1994) provided circumstantial evidence to this effect in their comparative study of differences in juvenile growth and patterns of length bimodality in Scottish and Spanish Atlantic salmon. Intriguingly, based on the results of a field-transplant experiment in Japan, Morita *et al.*'s (2009) work on white-spotted charr, *Salvelinus leucomaenis*, suggests that threshold reaction norms may, in themselves, exhibit plasticity; despite a common genetic origin for their charr, thresh-

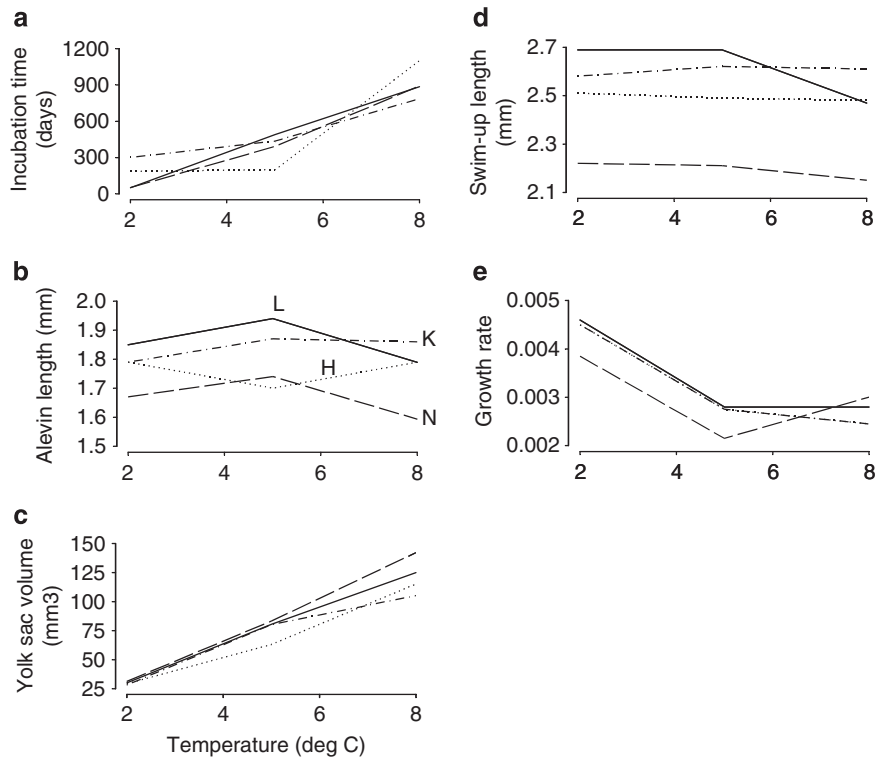


Figure 6 Reaction norms for early life-history traits for four Danish populations of brown trout, *Salmo trutta*, as a function of temperature (2, 5 and 8 °C): Norring Møllebæk River (N: long-dashed lines); Lilleaa River (L: solid lines); Karup River (K: dot-dashed lines); and Lake Hald: (H: dotted lines). Variables examined included (a) incubation time (days), (b) alevin length (mm), (c) yolk-sac volume, (d) swim-up length (mm) and (e) growth rate. The *y* axis represents residuals from linear regressions of each variable against egg weight, to minimise or remove maternal effects. Data re-drawn from Jensen *et al.* (2008).

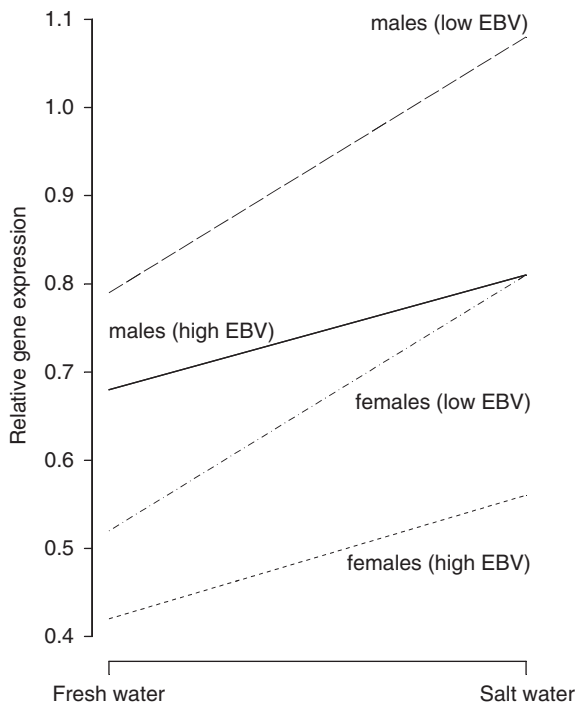


Figure 7 Reaction norms for relative gene expression of growth hormone receptor in brook trout, *Salvelinus fontinalis*, reared in freshwater and salt water (20 ppt) environments. Solid line: males of high estimated breeding value (EBV); long-dashed line: males of low EBV; dotted line: females of high EBV; dot-dashed line: females of low EBV. Data re-drawn from Côté *et al.* (2007).

olds for maturity differed among groups transplanted to sites that differed in stream width (Figure 8c).

Bivariate reaction norms

Patterns of association between age and size at maturity are the most commonly studied bivariate reaction norms, and the most common of these are probabilistic maturation reaction norms or PMRNs (rare studies of PMRNs in salmonids include those by Morita and Fukuwaka (2007) on Japanese chum salmon and by Kinnison *et al.* (2011) on New Zealand Chinook salmon). Given that PMRNs estimate the probability that an individual that has reached a specific age and size matures at that age and size, they are implicitly representative of univariate threshold reaction norms when each trait is considered separately. These probabilistic bivariate reaction norms have been employed with tremendous influence in the study of fisheries-induced evolution (for example, Heino *et al.*, 2002; Olsen *et al.*, 2004; Dunlop *et al.*, 2009). By controlling for the effects of growth rate on maturation, PMRNs have the potential to control for the effects of phenotypic plasticity on life-history traits, such that temporal changes in PMRNs might be indicative of genetic change (Dieckmann and Heino, 2007). However, while PMRNs are almost certainly reflective of some degree of genetic change within some populations, there is uncertainty in the degree to which shifts in PMRNs can generally be considered indicative of evolution (for example, Kuparinen and Merilä, 2007, 2008; Morita *et al.*, 2009; Uusi-Heikkilä *et al.*, 2011).

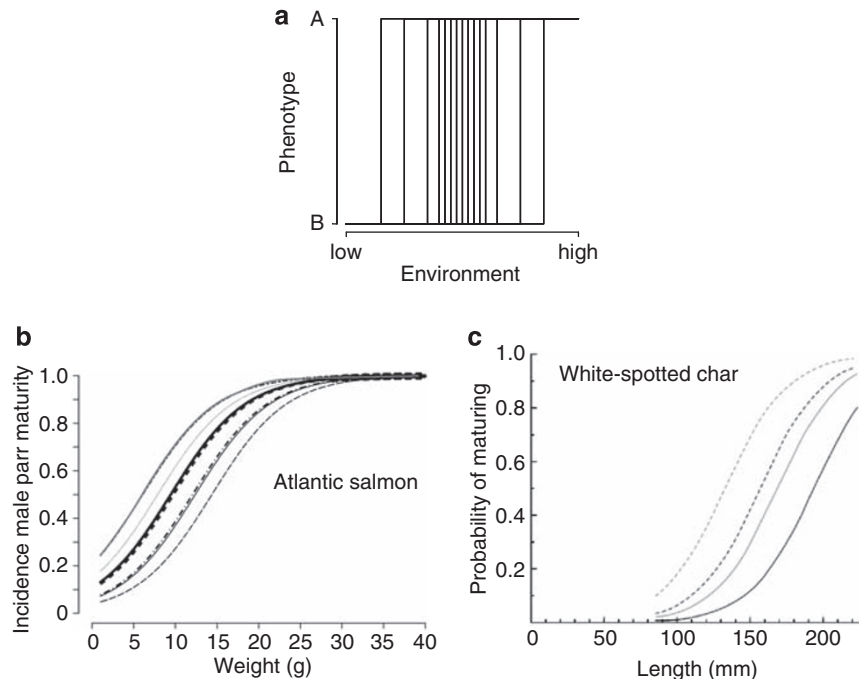


Figure 8 Threshold reaction norms for the adoption of alternative life histories: (a) hypothesised genetic variability in reaction norm switch-points between life histories A and B within a single population (re-drawn from Hazel *et al.*, 1990); (b) genetic differences in reaction norms for parr maturity in male Atlantic salmon, *Salmo salar*, as a function of growth rate (weight at 7 months) (original source: Piché *et al.*, 2008); and (c) environmental differences in reaction norms for maturity in white-spotted char, *Salvelinus leucomaenis*, as a function of growth rate (length at 1+ years) (original source: Morita *et al.*, 2009).

Although not explicitly addressing life-history variability in salmonids, Stearns and Koella's (1986) theoretically derived reaction norms for age and size at maturity provide templates for interpreting reaction norm variability in this family of fishes (Figure 9a). Specifically, they hypothesised that the association between individual growth rate and mortality was the primary determinant of shape variability in bivariate maturation reaction norms. On the basis of field data for individual growth, life history and mortality for three Newfoundland (Canada) populations of brook trout, Hutchings (1993b) constructed multivariate reaction norms for age, size and reproductive effort at maturity (Figure 9b) as part of an attempt (of arguably limited utility) to predict how fishing mortality might influence the shapes of life-history reaction norms and subsequent yields to fisheries. Haugen (2000) documented significant differences in maturation reaction norms for age and size at maturity among five populations of Norwegian grayling (Figure 9c). Although genetic differentiation in bivariate maturation reaction norms has yet to be documented in salmonids in a common-garden experiment, it seems highly probable that such work is imminent.

Issues arising

Fitness consequences of phenotypic change effected by reaction norms

Surprisingly, little attention has focussed on the question of how reaction norm slopes and elevations are related to individual fitness and, thus, population viability and persistence, a deficiency noted by several authors (Hutchings, 2004; Hutchings and Fraser, 2008; Chevin *et al.*, 2010; Reed *et al.*, 2010). For salmonid fishes, the question

appears to have been explored initially in a modelling study of age-at-maturity reaction norms in brook trout on Cape Race, Newfoundland. On the basis of field-estimated age-specific schedules of survival and fecundity, and using the per-capita rate of population growth, r , as a measure of average individual fitness, Hutchings (1996) estimated the ages at maturity that maximised fitness along a gradient of individual growth. The fitness functions that emerged from this work were generally consistent with the prediction that early maturity is favoured by rapid growth and delayed maturity by slower growth. However, the fitness benefits to slow-growing trout of delaying maturity were shown to decline with reductions in survival attributable to external environmental factors, such that all trout in the population that experienced the highest mortality were favoured to mature at an early age, irrespective of their growth.

This apparently novel prediction that high adult mortality favours invariant reaction norms for age at maturity appears to be consistent with Haugen's (2000) report of invariance in age at maturity within a high-mortality grayling population and may be concordant with temporal changes in the slopes of PMRNs in heavily harvested fish populations. Subsequent to the Newfoundland trout research, the only study in fishes (albeit not salmonids) to estimate the fitness associated with different positions along a reaction norm would appear to be McCairns and Bernatchez's (2010) work on genotype \times environment interactions in gene expression in threespine sticklebacks, *Gasterosteus aculeatus*.

To illustrate this point further, consider the linear reaction norms (solid lines) depicted in Figure 10. As the phenotype changes along the positively linear reaction norm, the fitness of the genotype (dashed lines) may change as well, in a linear (w_1) or nonlinear (w_2) manner,

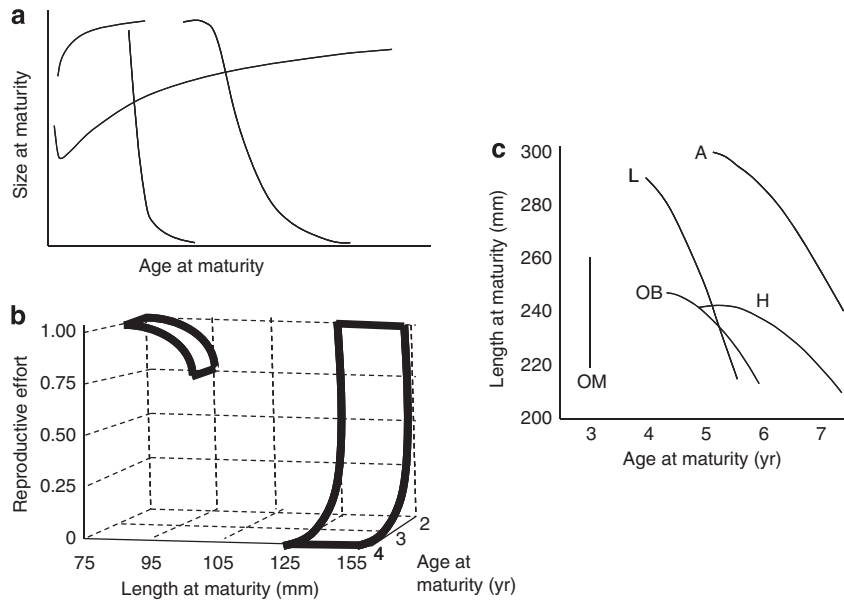


Figure 9 Bivariate or multivariate reaction norms for maturity: (a) four predicted bivariate reaction norms between age and size at maturity that depend on the relationship between growth rate and mortality (re-drawn from Stearns and Koella, 1986); (b) multivariate reaction norms (delineated by thick black lines) for age, size and reproductive effort at maturity for two Newfoundland populations of brook trout, *Salvelinus fontinalis*: Freshwater River (left reaction norm) and Cripple Cove River (right reaction norm) (data re-drawn from Hutchings, 1993b); and (c) bivariate reaction norms for age and size at maturity for five populations of grayling, *Thymallus thymallus*, in Norway (data re-drawn from Haugen, 2000) (A, Aursjøen; H, Hårrtjønn; L, Lesjaskogsvatn; OB, Osbumagasinet; OM, Øvre Mærrabottvatn).

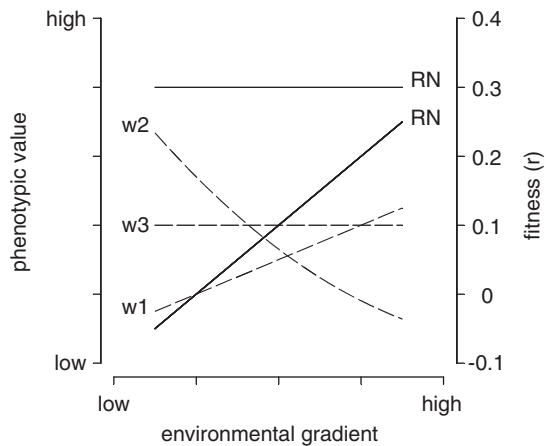


Figure 10 Hypothetical norms of reaction (RN; solid lines) and associated hypothetical fitness functions (dashed lines). Irrespective of whether the reaction norm has a zero (upper reaction norm) or non-zero slope, as the environmental gradient changes from low to high levels, the fitness associated with phenotypic change stipulated by the reaction norm may increase (w_1), decline (w_2) or remain constant (w_3). Note that fitness is expressed here as r (the per-capita rate of population growth) and that the fitness functions with non-zero slopes encompass values of r less than 0.

or it may remain constant (w_3). As Figure 10 is also meant to illustrate, changes in fitness may be realised irrespective of whether the reaction norm has a non-zero slope or not. The point here is that the slope of the reaction norm itself (with the possible exception of some norms of reaction for survival) does not provide reliable information on how plasticity affects fitness. (Chevin *et al.* (2010) have produced an heuristically appealing interpretation of how fitness changes along reaction norms in their Figure 1b.)

One consequence of this uncertainty is that, in the absence of such information, it becomes very difficult to ascertain the adaptive value of variable levels of plasticity within a population. As a first approximation, one might assume that high levels of genotype \times environment interactions—reflected by highly variable reaction norm slopes—are indicative of high levels of responsiveness to environmental change and that such high genetic variability is a good thing. This assumption may be valid for some traits under some circumstances, but such an approximation overlooks the fact that plasticity can exact costs (for example, increased mortality associated with compensatory growth; Johnsson and Bohlin, 2006). A steep reaction norm slope may, for example, reflect a high level of developmental instability. By contrast, recent evidence of a lack of plasticity cost in salmonids (Morris *et al.*, 2011) underscores the fundamental point that if one does not measure the fitness consequences of variability in plasticity, the risk of drawing spurious conclusions concerning the adaptive significance of plasticity may be high.

Costs of plasticity: trade-offs and genetic correlations

Although substantive work has been directed to descriptions of plasticity at various levels of biological organisation in salmonids (for example, family, ecotype, population), there is a dearth of studies directed to understanding the trade-offs associated with reaction norms (Ghalambor *et al.*, 2007). This deficiency is by no means unique to fishes. Angilletta *et al.* (2003) argued persuasively that theories on the evolution of reaction norms need to incorporate trade-offs related to resource acquisition (as commonly considered in behavioural ecology), resource allocation (common to theories and predictions of life-history evolution) and trade-offs

resulting from specialisation for a given environment, such that an increase in performance within one range of environmental conditions is associated with a reduction in performance within another set of environmental conditions (a traditional focus of evolutionary physiologists).

Evolutionary reaction norm theory is generally silent on how selection responses in the plasticity of one trait might be linked with changes in the plasticity of a correlated trait (although to some degree this depends on whether one adopts a reaction-norm or character-state model of plasticity). Although it is acknowledged that genetic correlations are environment specific (Sgrò and Hoffman, 2004), the grounds for theoretically and empirically addressing questions related to genetic correlations and plasticity seem particularly fertile. For traits that are genetically correlated with one another, to what degree (if any) might the plasticity in these traits also be genetically correlated with one another? That is, if reaction norms are heritable entities, to what extent might the slopes and/or elevations of the reaction norms of one trait be genetically correlated with the slopes and/or elevations of the reaction norms of another trait? Indeed, to what extent are the slope and the elevation of the *same* reaction norm genetically correlated (Nussey *et al.*, 2005)? How might increases or reductions in the plasticity of one trait affect the plasticity of a genetically correlated trait?

Answers to these questions ultimately pertain to factors that constrain the magnitude and rate of evolutionary change that reaction norms might experience under various forms of selection.

Responses to natural and human-induced selection

Selection experiments are invaluable to the study of evolution. In theory, they allow one to evaluate the magnitude of selection responses, the consequences to the mean and variance in per-capita population growth rate and the correlated responses in the average values, and in the plasticity, of other traits. However, the intractability of conducting selection experiments on many fishes, including salmonids, necessitates the use of models to predict how reaction norms might respond to natural and anthropogenic selection pressures.

As noted above, PMRNs have been used extensively to test the hypothesis that fishing has generated evolution in exploited populations. Although temporal shifts in PMRNs have been reported for a number of harvested fish populations (Dieckmann and Heino, 2007; Hutchings and Fraser, 2008), a general framework for predicting the precise changes in life-history reaction norms resulting from increased fishing pressure seems to be lacking. Hutchings (1993b, 2004) used age-specific survival and fecundity data on brook trout to predict how reaction norms for age, size and effort at maturity might respond to increases in adult mortality. As fishing mortality increased, selection was predicted to favour a flattening of reaction norms, notably for age and effort at maturity, such that individuals would be favoured to reproduce as early in life as possible and to expend the maximum amount of effort at that age, irrespective of growth rate. As noted previously, these hypothesised changes in plasticity are consistent with differences in life-history reaction norms in salmonid populations for

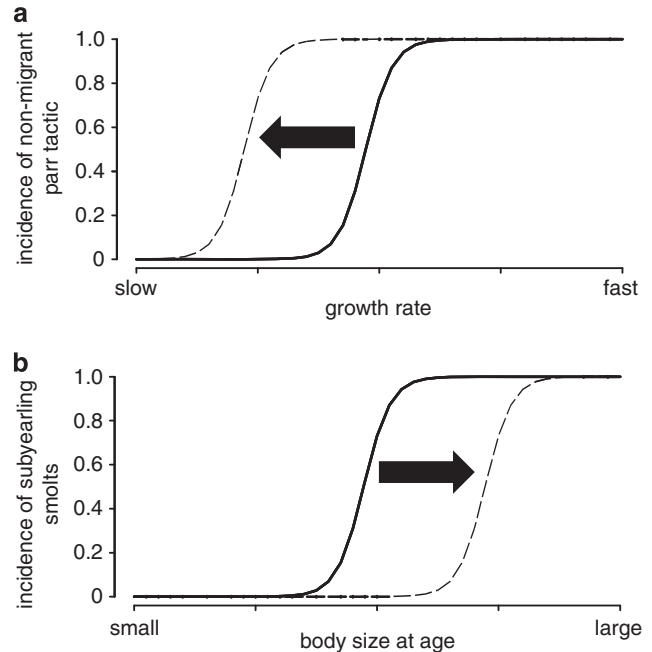


Figure 11 Hypothetical examples of human-induced evolution on threshold norms of reaction. In example (a), increased fishing mortality of male Atlantic salmon at sea would be predicted to increase the fitness of male parr that mature in the absence of a seaward migration. This might be reflected in a shift in the growth-rate threshold for parr maturity towards the left, lowering the growth rate required to attain parr maturity, and increasing the incidence of the parr tactic within the affected population *ceteris paribus*. In example (b), the construction of multiple dams is considered to have influenced the probability of survival by salmon smolts in the Columbia River, possibly resulting in an increase in the fitness associated with the tactic of migrating to sea as a yearling rather than as a sub-yearling. One mechanism by which a human-induced evolutionary shift could be effected is through an increase in the body size threshold required for the salmon to migrate to sea as sub-yearlings.

which survival data are available (Hutchings, 1996; Haugen, 2000). Thus, one might predict that increased fishing pressure would select for reduced levels of plasticity, leading to reaction norms having progressively shallower slopes (although it is worth noting that human-induced evolutionary changes in plasticity can be highly variable; Crispo *et al.*, 2010).

Anthropogenic selection on threshold reaction norms might also result in shifts in the switch-points that trigger the adoption of alternative life histories. Montgomery (1983), for example, suggested that increased fishing mortality at sea might increase the frequency of the Atlantic salmon parr reproductive tactic because of the reduced survival of seaward migrants and, presumably, the reduced concomitant fitness associated with anadromy. Notwithstanding Myers *et al.*'s (1986) objection, it is logical to conclude that increased mortality among anadromous males at sea would increase the fitness associated with the parr tactic, leading to a shift in the inflection points of the reaction norms to lower growth-rate thresholds, as hypothesised by Piché *et al.* (2008) for Atlantic salmon and by Thériault *et al.* (2008) for brook trout (Figure 11a).

Research on Snake River fall Chinook salmon in the Columbia River (northwestern US) suggests another

means by which human-induced selection might genetically shift threshold reaction norms. Williams *et al.* (2008) hypothesised that dams may have altered the probability of surviving the freshwater environment to such an extent that it has resulted in an increase in the incidence of, and fitness realised by, smolts migrating to sea as yearlings rather than as sub-yearlings. One mechanism by which a human-induced evolutionary shift could be effected is through an increase in the body size threshold required for salmon to migrate to sea as sub-yearling smolts (Figure 11b).

Questions, predictions and conclusions

One of the objectives of any review is that it will serve as a stimulus for further research. In that context, a series of questions, predictions and conclusions emerge, directly or indirectly, from this work. Although the questions can certainly be addressed in salmonid fishes, they are intended to be framed as generally as possible to increase their potential applicability to other fishes and other poikilotherms (see also Ghalambor *et al.*, 2007).

Reaction norm variability

- (1) How variable is plasticity among individuals within populations, among populations within species and among species within and among clades?
- (2) How genetically variable are the shapes of reaction norms (that is, their slopes and elevations) within populations? To what extent do families within populations differ in their average response to environmental change?
- (3) To what extent does interbreeding (for example, between different wild populations, or between wild and domesticated populations) affect the shapes (and adaptive value) of reaction norms?
- (4) Are behavioural traits more plastic (steeper reaction-norm slopes) than morphological and life-history traits?

Selection

- (5) What is the additive component of genetic variability (that is, the heritability) in the slopes and elevations of reaction norms?
- (6) How rapidly do reaction norms respond to natural and anthropogenic selection?
- (7) Under what circumstances might the slopes of reaction norms evolve at a slower rate than the elevations of reaction norms?
- (8) Are the heritabilities of traits correlated with the heritability in the plasticity of those traits?

Constraints

- (9) Are the slope and elevation of the same reaction norm genetically correlated with one another?
- (10) Are there genetic correlations between the plasticity of one trait and the plasticity of another trait?
- (11) Are the shapes (and/or slopes) of reaction norms for some traits (or classes of traits) constrained to greater degrees (and express less variability) than others?
- (12) What are the causal mechanisms underlying plasticity from a physiological, hormonal and genetic perspective? How might these mechanisms constrain evolutionary shifts in plasticity?

Demographic and conservation consequences

- (13) How does individual fitness and, by extension, rate of per capita population growth change as phenotypes shift along norms of reaction?
- (14) What are the fitness costs associated with trait plasticity?
- (15) Are large populations more phenotypically plastic than small populations?
- (16) How might plasticity (for example, reaction-norm slope variability) change with abundance (for example, linearly, asymptotically)?
- (17) How does inbreeding and outbreeding affect trait plasticity? How might inbreeding and outbreeding depression affect the shapes of reaction norms?

Genetic markers and correlates of plasticity

- (18) Is population genetic variability, as reflected by variation at selectively neutral loci, correlated with trait plasticity?
- (19) Can genome surveys of molecular marker polymorphisms be used to identify candidate genes responsible for plasticity and reaction norm variability?
- (20) How does plasticity affect gene expression and gene transcription?

On the basis of the breadth of salmonid research on reaction norms undertaken thus far, one might conclude that light is increasingly being shed on answers to a small subset of these questions, beginning with information on plasticity among families (for example, Beacham and Murray, 1985, 1986a,b), continuing with work documenting genetic differences in reaction norms among populations (for example, Haugen and Vøllestad, 2000; Fraser *et al.*, 2008; Piché *et al.*, 2008; Evans *et al.*, 2010), and continuing further with recent initiatives to document plasticity in gene expression and transcription (Côté *et al.*, 2007; Aubin-Horth and Renn, 2009). Notwithstanding the progress that has been made in recent years, much remains to be done to further our understanding of the adaptive significance, constraints/costs and selection of reaction norms, and of the consequences of reaction-norm variability to population viability and conservation biology.

To conclude, the persistence of a species depends on the resistance and resilience of its populations to anthropogenic and natural environmental perturbation (Hutchings *et al.*, 2007; Schindler *et al.*, 2010). Thus, in addition to increasing our understanding of how genotype \times environment interactions influence evolution (Blackburn and Schneider, 1994; Sultan and Stearns, 2005; Crispo, 2008), studies of genetic variability in phenotypic plasticity should serve to refine our capacity to predict how organisms will respond adaptively to new environments (Ghalambor *et al.*, 2007), including those resulting from climate change (Nussey *et al.*, 2005; Visser, 2008; Reed *et al.*, 2010). Although reaction-norm research in salmonids might be described as being in its infancy from a numerical publication perspective, a strong argument can be made that it has matured sufficiently to permit some degree of generalisation. Work undertaken to date has also provided a sufficiently strong theoretical and empirical foundation upon which unexplored questions, such as those referred to above, might be addressed and future research initiatives undertaken.

Being mindful of a publication bias that might render genetic differences in reaction norms more likely to be reported than not, there would appear to be ample evidence of genetic differentiation in reaction norms among individuals, among families and among populations in salmonid fishes. Although firm evidence of additive genetic variability in salmonid plasticity has yet to be reported, it seems highly probable that such variability exists and that selection (both natural and anthropogenic) can act, and has acted, upon reaction norms. This review would suggest that there is ample intellectual grist for re-bottling the century-old concept of reaction norms into the new research opportunities proffered by the extraordinarily plastic family of salmonid fishes.

Conflict of interest

The author declares no conflict of interest.

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References

- Alm G (1959). Connection between maturity, size, and age in fishes. *Rep Inst Freshw Res Drottningholm* **40**: 1–145.
- Andreeva AP, Makhrov AA, Kuzishchin KV, Novikov GG (1996). Adaptive changes of lactate dehydrogenase in white skeletal muscle of the sea trout *Salmo trutta* L. *Izvest Akad Nauk Ser Biol* **4**: 406–410.
- Angilletta MJ, Wilson RS, Navas CA, James RS (2003). Tradeoffs and the evolution of thermal reaction norms. *Trends Ecol Evol* **18**: 234–240.
- Aubin-Horth N, Bourque JF, Daigle G, Hedger R, Dodson JJ (2006). Longitudinal gradients in threshold sizes for alternative male life history tactics in a population of Atlantic salmon (*Salmo salar*). *Can J Fish Aquat Sci* **63**: 2067–2075.
- Aubin-Horth N, Dodson JJ (2004). Influence of individual body size and variable thresholds on the incidence of a sneaker male reproductive tactic in Atlantic salmon. *Evolution* **58**: 136–144.
- Aubin-Horth N, Letcher BH, Hofmann HA (2009). Gene-expression signatures of Atlantic salmon's plastic life cycle. *Gen Comp Endocrinol* **163**: 278–284.
- Aubin-Horth N, Renn SCP (2009). Genomic reaction norms: using integrative biology to understand molecular mechanisms of phenotypic plasticity. *Mol Ecol* **18**: 3763–3780.
- Bailey JK, Saunders RL, Buzeta MI (1980). Influence of parental smolt age and se age on growth and smolting of hatchery-reared Atlantic salmon (*Salmo salar*). *Can J Fish Aquat Sci* **37**: 1379–1386.
- Baldwin JM (1896). A new factor in evolution. *Am Nat* **30**: 441–451, 536–553.
- Baum D, Laughton R, Armstrong JD, Metcalfe NB (2004). Altitudinal variation in the relationship between growth and maturation rate in salmon parr. *J Anim Ecol* **73**: 253–260.
- Basak SL, Chaudhuri BB (1967). Genetic variation and phenotypic plasticity of roots in two cultivated species of jute (*Corchorus olitorus* L. and *C. capsularis* L.). *Biol Plant* **9**: 292–300.
- Beacham TD (1988). A genetic analysis of early development in pink (*Oncorhynchus gorbuscha*) and chum salmon (*Oncorhynchus keta*) at three different temperatures. *Genome* **30**: 89–96.
- Beacham TD, Murray CB (1985). Effect of female size, egg size, and water temperature on developmental biology of chum salmon (*Oncorhynchus keta*) from the Nitinat River, British Columbia. *Can J Fish Aquat Sci* **42**: 1755–1765.
- Beacham TD, Murray CB (1986a). Comparative developmental biology of link salmon, *Oncorhynchus gorbuscha*, in southern British Columbia. *J Fish Biol* **28**: 233–246.
- Beacham TD, Murray CB (1986b). The effect of spawning time and incubation temperature on meristic variation in chum salmon (*Oncorhynchus keta*). *Can J Zool* **64**: 45–48.
- Beacham TD, Murray CB (1989). Variation in developmental biology of sockeye salmon (*Oncorhynchus nerka*) and chinook salmon (*O. tshawytscha*) in British Columbia. *Can J Zool* **67**: 2081–2089.
- Beacham TD, Murray CB (1990). Temperature, egg size, and development of embryos and alevins of five species of Pacific salmon: a comparative analysis. *Trans Am Fish Soc* **119**: 927–945.
- Beckman BR, Dickhoff WW (1998). Plasticity of smolting in spring chinook salmon: relation to growth and insulin-like growth factor-I. *J Fish Biol* **53**: 808–826.
- Bernatchez L, Renaut S, Whiteley AR, Derome N, Jeukens J, Landry L *et al.* (2010). On the origin of species: insights from the ecological genomics of lake whitefish. *Philos Trans R Soc Ser B* **365**: 1783–1800.
- Blackburn DG, Schneider CW (1994). Old wine in a new bottle: evolution by another name. *J Theor Biol* **171**: 233–237.
- Bohlin T, Dellefors C, Feremo U (1990). Large or small at maturity—theories on the choice of alternative male strategies in anadromous salmonids. *Ann Zool Fennici* **27**: 139–147.
- Bradford GE (1969). Genetic control of ovulation rate and embryo survival in mice. I. Response to selection. *Genetics* **61**: 905–921.
- Bradshaw AD (1965). Evolutionary significance of phenotypic plasticity in plants. *Adv Genet* **13**: 115–155.
- Chevin L-M, Lande R, Mace GM (2010). Adaptation, plasticity, and extinction in a changing environment: towards a predictive theory. *PLoS Biol* **8**: e1000357.
- Côté G, Perry G, Blier P, Bernatchez L (2007). The influence of gene–environment interactions non GHR and IGF-I expression and their association with growth in brook charr, *Salvelinus fontinalis* (Mitchill). *BMC Gen* **8**: 87.
- Crispo E (2008). Modifying effects of phenotypic plasticity on interactions among natural selection, adaptation and gene flow. *J Evol Biol* **21**: 1460–1469.
- Crispo E, DiBattista JD, Correa C, Thibert-Plante X, McKellar AE, Schwartz AK *et al.* (2010). The evolution of phenotypic plasticity in response to anthropogenic disturbance. *Evol Ecol Res* **12**: 47–66.
- Croisetièrre S, Bernatchez L, Bellhumeur P (2010). Temperature and length-dependent modulation of the MH class II β gene expression in brook charr (*Salvelinus fontinalis*) by a cis-acting minisatellite. *Mol Immunol* **47**: 1817–1829.
- Darwish TL, Hutchings JA (2009). Genetic variability in reaction norms between farmed and wild backcrosses of Atlantic salmon *Salmo salar*. *Can J Fish Aquat Sci* **66**: 83–90.
- de Jong G (1995). Phenotypic plasticity as a product of selection in a variable environment. *Am Nat* **145**: 493–512.
- de Jong G (2005). Evolution of phenotypic plasticity: patterns of plasticity and the emergence of ecotypes. *New Phytol* **166**: 101–117.
- Dieckmann U, Heino M (2007). Probabilistic maturation reaction norms: their history, strengths, and limitations. *Mar Ecol Prog Ser* **335**: 253–269.
- Dobzhansky T (1937). *Genetics and the Origin of Species*. Columbia: New York.

- Dunlop ES, Heino M, Dieckmann U (2009). Eco-genetic modeling of contemporary life-history evolution. *Ecol Applic* **19**: 1815–1834.
- Einum S, Fleming IA (1999). Maternal effects of egg size in brown trout (*Salmo trutta*): norms of reaction to environmental quality. *Proc R Soc B* **266**: 2095–2100.
- Elson PF (1957). The importance of size in the change from parr to smolt in Atlantic salmon. *Can Fish Cult* **21**: 1–6.
- Eskelinen P (1989). Effects of different diets on egg production and egg quality of Atlantic salmon (*Salmo salar* L.). *Aquaculture* **79**: 275–281.
- Evans ML, Neff BD, Heath DD (2010). Quantitative genetic and translocation experiments reveal genotype-by-environment effects on juvenile life-history traits in two populations of Chinook salmon (*Oncorhynchus tshawytscha*). *J Evol Biol* **23**: 687–698.
- Falconer DS (1960). *Introduction to Quantitative Genetics*. Oliver & Boyd: Edinburgh.
- Fleming IA (1996). Reproductive strategies of Atlantic salmon: ecology and evolution. *Rev Fish Biol Fish* **6**: 379–416.
- Fraser DJ, Cook AM, Eddington JD, Bentzen P, Hutchings JA (2008). Mixed evidence for reduced local adaptation in wild salmon resulting from interbreeding with escaped farmed salmon: complexities in hybrid fitness. *Evol Applic* **1**: 501–512.
- Fraser DJ, Weir LK, Darwish TL, Eddington JD, Hutchings JA (2007). Divergent compensatory growth responses within species: linked to contrasting migrations in salmon? *Oecologia* **153**: 543–553.
- Fukuwaka MA, Morita K (2008). Increase in maturation size after the closure of a high seas gillnet fishery on hatchery-reared chum salmon *Oncorhynchus keta*. *Evol Applic* **1**: 376–387.
- Ghalambor CK, McKay JK, Carroll SP, Reznick DN (2007). Adaptive versus non-adaptive phenotypic plasticity and the potential for contemporary adaptation in new environments. *Funct Ecol* **21**: 394–407.
- Glebe BD, Saunders RL, Sreedharan A (1978). Genetic and environmental influence in expression of precocious sexual maturity of hatchery-reared Atlantic salmon (*Salmo salar*) parr. *Can J Gen Cytol* **20**: 444.
- Goldschmidt RB (1940). *The Material Basis of Evolution*. Yale University Press: New Haven.
- Gordon DM, Matson PA (1991). Interactions of behavioral and evolutionary ecology in changing environments. *Ecology* **72**: 1179.
- Gross MR (1985). Disruptive selection for alternative life histories in salmon. *Nature* **313**: 47–48.
- Haugen TO (2000). Growth and survival effects on maturation pattern in populations of grayling with recent common ancestors. *Oikos* **90**: 107–118.
- Haugen TO, Vøllestad LA (2000). Population differences in early life-history traits in grayling. *J Evol Biol* **13**: 897–905.
- Hazel WN, Smock R, Johnson MD (1990). A polygenic model for the evolution and maintenance of conditional strategies. *Proc R Soc B* **242**: 181–187.
- Healey MC (1991). Life history Chinook salmon. In: Groot C, Margolis L (eds). *Pacific Salmon life Histories*. UBC Press: Vancouver, pp 313–393.
- Heino M, Dieckmann U, Godø OR (2002). Measuring probabilistic reaction norms for age and size at maturation. *Evolution* **56**: 669–678.
- Hendry AP, Hensleigh JE, Reisenbichler RR (1998). Incubation temperature, developmental biology, and the divergence of sockeye salmon (*Oncorhynchus nerka*) within Lake Washington. *Can J Fish Aquat Sci* **55**: 1387–1394.
- Hendry AP, Stearns SC (2004). *Evolution Illuminated: Salmon and their Relatives*. Oxford University Press: New York.
- Hindar K, Jonsson B, Ryman N, Ståhl G (1992). Genetic relationships among landlocked, resident, and anadromous brown trout, *Salmo trutta* L. *Heredity* **66**: 83–91.
- Hutchings JA (1993a). Behavioural implications of intraspecific life history variation. *Mar Behav Physiol* **23**: 187–203.
- Hutchings JA (1993b). Reaction norms for reproductive traits in brook trout and their influence on life history evolution effected by size-selective harvesting. In: Stokes TK, McGlade JM, Law R (eds). *The Exploitation of Evolving Resources*. Springer: Berlin, pp 107–125.
- Hutchings JA (1996). Adaptive phenotypic plasticity in brook trout, *Salvelinus fontinalis*, life histories. *Ecoscience* **3**: 25–32.
- Hutchings JA (2004). Norms of reaction and phenotypic plasticity in salmonid life histories. In: Hendry AP, Stearns SC (eds). *Evolution Illuminated: Salmon and Their Relatives*. Oxford University Press: New York, pp 154–174.
- Hutchings JA, Fraser DJ (2008). The nature of fishing- and farming-induced evolution. *Mol Ecol* **17**: 294–313.
- Hutchings JA, Myers RA (1988). Mating success of alternative maturation phenotypes in male Atlantic salmon, *Salmo salar*. *Oecologia* **75**: 169–174.
- Hutchings JA, Myers RA (1994). The evolution of alternative mating strategies in variable environments. *Evol Ecol* **8**: 256–268.
- Hutchings JA, Jones MEB (1998). Life history variation and growth rate thresholds for maturity in Atlantic salmon, *Salmo salar*. *Can J Fish Aquat Sci* **55**(Suppl 1): 22–47.
- Hutchings JA, Swain DP, Rowe S, Eddington JD, Puvanendran V, Brown JA (2007). Genetic variation in life-history reaction norms in a marine fish. *Proc R Soc B* **274**: 1693–1699.
- Jensen LF, Hansen MM, Pertoldi C, Holdensgaard G, Dons Mensberg K-L, Loeschke V (2008). Local adaptation in brown trout early life-history traits: implications for climate change adaptability. *Proc R Soc B* **275**: 2859–2868.
- Johannsen W (1911). The genotype conception in heredity. *Am Nat* **45**: 129–159.
- Johnson RK, Nielsen MK, Casey DS (1999). Responses in ovulation rate, embryonal survival, and litter traits in swine to 14 generations of selection to increase litter size. *J Anim Sci* **77**: 541–557.
- Johnsson JI, Bohlin T (2006). The cost of catching up: increased winter mortality following structural growth compensation in the wild. *Proc R Soc B* **273**: 1281–1286.
- Jones JW (1959). *The Salmon*. Collins: London.
- Kinnison MT, Unwin MJ, Hershberger WK, Quinn TP (1998). Egg size, fecundity, and development rate of two introduced New Zealand chinook salmon (*Oncorhynchus tshawytscha*) populations. *Can J Fish Aquat Sci* **55**: 1946–1953.
- Kinnison MT, Quinn TP, Unwin MJ (2011). Correlated contemporary evolution of life history traits in New Zealand Chinook salmon, *Oncorhynchus tshawytscha*. *Heredity* **106**: 448–459.
- Klemetsen A, Amundsen PA, Dempson JB, Jonsson B, Jonsson N, O'Connell MF *et al.* (2003). Atlantic salmon *Salmo salar* L., brown trout *Salmo trutta* L. and Arctic charr, *Salvelinus alpinus* (L.): a review of aspects of their life histories. *Ecol Freshw Fish* **12**: 1–59.
- Kuparinen A, Merilä J (2007). Detecting and managing fisheries-induced evolution. *Trends Ecol Evol* **22**: 652–659.
- Kuparinen A, Merilä J (2008). The role of growth history in determining age and size at maturation in exploited fish populations. *Fish Fisheries* **9**: 201–207.
- Lande R (2009). Adaptation to an extraordinary environment by evolution of phenotypic plasticity and genetic assimilation. *J Evol Biol* **22**: 1435–1446.
- Latta RG, Gardner KM, Johansen-Morris AD (2007). Hybridization, recombination, and the genetic basis of fitness variation across environments in *Avena barbata*. *Genetica* **129**: 167–177.
- Leonardsson K, Lundberg P (1986). The choice of reproductive tactics as mixed evolutionarily stable strategy: the case of male Atlantic salmon (*Salmo salar* L.). *Rept Inst Freshw Res Drottningholm* **63**: 69–76.
- McCairns RJS, Bernatchez L (2010). Adaptive divergence between freshwater and marine sticklebacks: insights into the role of phenotypic plasticity from an integrated analysis of candidate gene expression. *Evolution* **64**: 1029–1047.

- McLaughlin RL, Grant JWA (1994). Morphological and behavioural differences among recently-emerged brook charr, *Salvelinus fontinalis*, foraging in slow- vs fast-running water. *Environ Biol Fish* **39**: 289–300.
- Metcalfe NB (1993). Behavioral causes and consequences of life-history variation in fish. *Mar Behav Physiol* **23**: 205–217.
- Metcalfe NB, Huntingford FA, Graham WD, Thorpe JE (1989). Early social status and the development of life-history strategies in Atlantic salmon. *Proc R Soc B* **236**: 7–19.
- Montgomery WL (1983). Parr excellence. *Nat Hist* **92**: 58–67.
- Morita K, Fukuwaka M (2007). Why age and size at maturity have changed in Pacific salmon. *Mar Ecol Prog Ser* **335**: 289–294.
- Morita K, Nagasawa T (2010). Latitudinal variation in the growth and maturation of masu salmon (*Oncorhynchus masou*) parr. *Can J Fish Aquat Sci* **67**: 955–965.
- Morita K, Tsuboi J-I, Nagasawa T (2009). Plasticity in probabilistic reaction norms for a salmonid fish. *Biol Lett* **5**: 628–631.
- Morris MRJ, Fraser DJ, Eddington JD, Hutchings JA (2011). Hybridization effects on phenotypic plasticity: experimental compensatory growth responses in farmed-wild Atlantic salmon. *Evol Applic* (in press).
- Murray CB, Beacham TD (1987). The development of chinook (*Oncorhynchus tshawytscha*) and chum salmon (*Oncorhynchus keta*) embryos and alevins under varying temperature regimes. *Can J Zool* **65**: 2672–2681.
- Murray CB, Beacham TD, McPhail JD (1990). Influence of parental stock and incubation temperature on the early development of coho salmon (*Oncorhynchus kisutch*) in British Columbia. *Can J Zool* **68**: 347–358.
- Myers RA, Hutchings JA (1986). Selection against parr maturation in Atlantic salmon. *Aquaculture* **53**: 313–320.
- Myers RA, Hutchings JA, Gibson RJ (1986). Variation in male parr maturation within and among populations of Atlantic salmon, *Salmo salar*. *Can J Fish Aquat Sci* **43**: 1242–1248.
- Nath S, Kales S, Fujiki K, Dixon B (2006). Major histocompatibility class II genes in rainbow trout (*Oncorhynchus mykiss*) exhibit temperature dependent down-regulation. *Immunogenetics* **58**: 443–453.
- Nelson JS (2006). *Fishes of the World*. Wiley: New York.
- Nicieza AG, Reyes-Gavilán FG, Braña F (1994). Differentiation in juvenile growth and bimodality patterns between northern and southern populations of Atlantic salmon (*Salmo salar* L.). *Can J Zool* **72**: 1603–1610.
- Nussey DH, Postma E, Gienapp P, Visser ME (2005). Selection on heritable phenotypic plasticity in a wild bird population. *Science* **310**: 304–306.
- Okamoto KW, Whitlock R, Magnan P, Dieckmann U (2009). Mitigating fisheries-induced evolution in lacustrine brook charr (*Salvelinus fontinalis*) in southern Quebec, Canada. *Evol Applic* **2**: 415–437.
- Olsen EM, Heino M, Lilly GR, Morgan MJ, Brattey J, Ernande B *et al.* (2004). Maturation trends indicative of rapid evolution preceded the collapse of northern cod. *Nature* **428**: 932–935.
- Peres-Neto PR, Magnan P (2004). The influence of swimming demand on phenotypic plasticity and morphological integration: a comparison of two polymorphic charr species. *Oecologia* **140**: 36–45.
- Piché J, Hutchings JA, Blanchard W (2008). Genetic variation in threshold reaction norms for alternative reproductive tactics in male Atlantic salmon, *Salmo salar*. *Proc R Soc B* **275**: 1517–1574.
- Proulx R, Magnan P (2004). Contribution of phenotypic plasticity and heredity to the trophic polymorphism of lacustrine brook charr (*Salvelinus fontinalis*, M.). *Evol Ecol Res* **6**: 503–522.
- Quinn TP (2005). *The Behavior and Ecology of Pacific Salmon and Trout*. University of Washington Press: Seattle.
- Quinn TP, Doctor K, Kendall N, Rich HB (2009). Diadromy and the life history of sockeye salmon: nature, nurture, and the hand of man. *Am Fish Soc Symp* **69**: 23–42.
- Reed TE, Waples RS, Schindler DE, Hard JJ, Kinnison MT (2010). Phenotypic plasticity and population viability: the importance of environmental predictability. *Proc R Soc B* **277**: 3391–3400.
- Reznick DN (1993). Norms of reaction in fishes. In: Stokes TK, McGlade JM, Law R (eds). *The Exploitation of Evolving Resources*. Springer: Berlin, pp 72–90.
- Robinson BW, Wilson DS (1994). Character release and displacement in fishes: a neglected literature. *Am Nat* **144**: 596–627.
- Roff DA (1996). The evolution of threshold traits in animals. *Quart Rev Biol* **71**: 3–35.
- Rungruangsak-Torrissen K, Pringle GM, Moss R, Houlihan DF (1998). Effects of varying rearing temperatures on expression of different trypsin isozymes, feed conversion efficiency and growth in Atlantic salmon (*Salmo salar*). *Fish Physiol Biochem* **19**: 247–255.
- Sandlund OT, Gunnarsson K, Jónasson PM, Jonsson B, Lindem T, Magnússon KP *et al.* (1992). The arctic char *Salvelinus alpinus* in Lake Thingvallavatn. *Oikos* **64**: 305–351.
- Saunders RL, Henderson EB, Glebe BD (1982). Precocious sexual maturation and smoltification in male Atlantic salmon (*Salmo salar*). *Aquaculture* **28**: 211–229.
- Scheiner SM (2002). Selection experiments and the study of phenotypic plasticity. *J Evol Biol* **15**: 889–898.
- Schindler DE, Hilborn R, Chasco B, Boatright CP, Quinn TP, Rogers LA *et al.* (2010). Population diversity and the portfolio effect in an exploited species. *Nature* **465**: 609–612.
- Schlichting CD, Pigliucci M (1998). *Phenotypic Evolution: A Reaction Norm Perspective*. Sinauer: Sunderland, MA.
- Schmalhausen II (1949). *Factors of Evolution*. Blakiston: Philadelphia.
- Sgrò CM, Hoffman AA (2004). Genetic correlations, tradeoffs and environmental variation. *Heredity* **93**: 241–248.
- Shields BA, Underhill JC (1993). Phenotypic plasticity of a transplanted population of dwarf cisco, *Coregonus artedii*. *Env Biol Fish* **37**: 9–23.
- Stearns SC (1989). The evolutionary significance of phenotypic plasticity. *BioScience* **39**: 436–445.
- Stearns SC, Koella JC (1986). The evolution of phenotypic plasticity in life-history traits: predictions of reaction norms for age and size at maturity. *Evolution* **40**: 893–913.
- Stickland NC, White RN, Mescall PE, Crook AR, Thorpe JE (1988). The effect of temperature on myogenesis in embryonic development of the Atlantic salmon (*Salmo salar* L.). *Anat Embryol* **178**: 253–257.
- Sultan SE, Stearns SC (2005). Environmentally contingent variation: phenotypic plasticity and norms of reaction. In: Hallgrímsson B, Hall B (eds). *Variation*. Elsevier: Boston, pp 303–332.
- Thériault V, Dunlop E, Dieckmann U, Bernatchez L, Dodson JJ (2008). The impact of fishing-induced mortality on the evolution of alternative life-history tactics in brook charr. *Evol Applic* **1**: 409–423.
- Thorpe JE (1986). Age at first maturity in Atlantic salmon, *Salmo salar*, freshwater period influences and conflicts with smolting. *Can Spec Pub Fish Aquat Sci* **89**: 7–14.
- Thorpe JE, Mangel M, Metcalfe NB, Huntingford FA (1998). Modelling the proximate basis of salmonid life-history variation, with application to Atlantic salmon, *Salmo salar* L. *Evol Ecol* **12**: 581–599.
- Tomkins JL, Hazel D (2007). The status of the conditional evolutionarily stable strategy. *Trends Ecol Evol* **22**: 522–528.
- Uusi-Heikkilä S, Kuparinen A, Wolter C, Meinelt T, O'Toole A, Arlinghaus R (2011). Experimental assessment of the probabilistic maturation reaction norm: condition matters. *Proc R Soc Lond B* (in press).

- Vainikka A, Kallio-Nyberg I, Heino M, Koljonen M-L (2009). Divergent trends in life-history traits between Atlantic salmon *Salmo salar* of wild and hatchery origin in the Baltic Sea. *J Fish Biol* **76**: 622–640.
- Via S, Gomulkiewicz R, de Jong G, Scheiner SM, Schlichting CD, van Tienderen PH (1995). Adaptive phenotypic plasticity: consensus and controversy. *Trends Ecol Evol* **10**: 212–217.
- Via S, Lande R (1985). Genotype–environment interaction and the evolution of phenotypic plasticity. *Evolution* **39**: 505–522.
- Visser ME (2008). Keeping up with a warming world; assessing the rate of adaptation to climate change. *Proc R Soc B* **275**: 649–659.
- Wang H-Y, Hook TO, Ebener MP, Mohr LC, Schneeberger PJ (2008). Spatial and temporal variation in maturation schedules of lake whitefish (*Coregonus clupeaformis*) in the Great Lakes. *Can J Fish Aquat Sci* **65**: 2157–2169.
- Williams JG, Zabel RW, Waples RS, Hutchings JA, Connor WP (2008). Potential for anthropogenic disturbances to influence evolutionary change in the life history of a threatened salmonid. *Evol Applic* **1**: 271–285.
- Woltereck R (1909). Weiterer experimentelle untersuchungen uber artveränderung, speziell uber das wesen quantitativer artunterschiede bei daphniden. *Versuch Deutsch Zool Gesellschaft* **19**: 110–172.