

# A critical review of adaptive genetic variation in Atlantic salmon: implications for conservation

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## ABSTRACT

Here we critically review the scale and extent of adaptive genetic variation in Atlantic salmon (*Salmo salar* L.), an important model system in evolutionary and conservation biology that provides fundamental insights into population persistence, adaptive response and the effects of anthropogenic change. We consider the process of adaptation as the end product of natural selection, one that can best be viewed as the degree of matching between phenotype and environment. We recognise three potential sources of adaptive variation: heritable variation in phenotypic traits related to fitness, variation at the molecular level in genes influenced by selection, and variation in the way genes interact with the environment to produce phenotypes of varying plasticity. Of all phenotypic traits examined, variation in body size (or in correlated characters such as growth rates, age of seaward migration or age at sexual maturity) generally shows the highest heritability, as well as a strong effect on fitness. Thus, body size in Atlantic salmon tends to be positively correlated with freshwater and marine survival, as well as with fecundity, egg size, reproductive success, and offspring survival. By contrast, the fitness implications of variation in behavioural traits such as aggression, sheltering behaviour, or timing of migration are largely unknown. The adaptive significance of molecular variation in salmonids is also scant and largely circumstantial, despite extensive molecular screening on these species. Adaptive variation can result in local adaptations (LA) when, among other necessary conditions, populations live in patchy environments, exchange few or no migrants, and are subjected to differential selective pressures. Evidence for LA in Atlantic salmon is indirect and comes mostly from ecological correlates in fitness-related traits, the failure of many translocations, the poor performance of domesticated stocks, results of a few common-garden experiments (where different populations were raised in a common environment in an attempt to dissociate heritable from environmentally induced phenotypic variation), and the pattern of inherited resistance to some parasites and diseases. Genotype  $\times$  environment

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interactions occur for many fitness traits, suggesting that LA might be important. However, the scale and extent of adaptive variation remains poorly understood and probably varies, depending on habitat heterogeneity, environmental stability and the relative roles of selection and drift. As maladaptation often results from phenotype-environment mismatch, we argue that acting as if populations are not locally adapted carries a much greater risk of mismanagement than acting under the assumption for local adaptations when there are none. As such, an evolutionary approach to salmon conservation is required, aimed at maintaining the conditions necessary for natural selection to operate most efficiently and unhindered. This may require minimising alterations to native genotypes and habitats to which populations have likely become adapted, but also allowing for population size to reach or extend beyond carrying capacity to encourage competition and other sources of natural mortality.

*Key words:* adaptive variation, local adaptation, heritabilities, phenotypic plasticity, genotype-by-environment interaction, fitness, conservation, Atlantic salmon, salmonids.

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## I. INTRODUCTION: ATLANTIC SALMON AS A MODEL SYSTEM FOR STUDYING ADAPTATIONS

Salmonids are well suited to address evolutionary questions (Stearns & Hendry, 2004) since they have relatively high fecundities, inhabit widely different habitats and have a tendency to reproduce in their home rivers, thus potentially giving rise to locally adapted populations (Allendorf & Waples, 1996). They have also been exploited since historical times, and are now farmed around the globe, which

has resulted in a wealth of information, possibly unparalleled in any other fish family. Yet, despite extensive knowledge of salmonid life histories and evolution (see recent contributions in Hendry & Stearns, 2004), the extent and scale of adaptive variation in salmonids remain the subject of debate (Bentsen, 1991, 1994; Adkison, 1995). The idea that salmon and trout may be locally adapted is not new (Calderwood, 1908; Huntsman, 1937; Ricker, 1972), but this view has until recently received only circumstantial support and continues to be challenged (e.g. Adkison, 1995; Purdom, 2001).

The last comprehensive review of adaptive variation in salmonids is 15 years old (Taylor, 1991), and since that seminal review several important advances have taken place. New technical developments have made it possible to have a more direct look at the relationship between genotype and phenotype, and the development of new hypervariable markers and parental assignment methods have greatly facilitated the study of natural salmon populations in the wild (e.g. Taggart *et al.*, 2001; Webb *et al.*, 2001; Garant *et al.*, 2002, 2003a). However, the last two decades have also witnessed an unprecedented growth in salmon aquaculture and a parallel decline in the abundance of wild salmon populations. Catches of Atlantic salmon have decreased by more than 80% to reach a historical low at the turn of the 21<sup>st</sup> century (WWF, 2001; ICES, 2005), while salmon farming has increased exponentially to make Atlantic salmon the fourth most valuable farmed fish species worldwide (FAO, 2004). Today, production of farmed Atlantic salmon exceeds wild Atlantic salmon catches by almost 600 times (ICES, 2005), an unparalleled situation in any fishery.

Problems posed by the large-scale farming of Atlantic salmon are numerous, both within its native range in the North Atlantic and elsewhere, where domesticated salmon escaping from fish farms may have contributed to the demise of their wild counterparts, or even of other endemic fish species (reviewed in WWF, 2005; Naylor *et al.*, 2005). Thus, while considerable advances have been made in adapting farmed salmon to live in captive conditions, dubbed *Salmo domesticus* by Gross (1998), relatively little is known about how wild salmon will respond to increasing anthropogenic pressures, how they may adapt to rapid climate change, or how fish farming will impact upon endangered wild salmon populations (Naylor *et al.*, 2005).

There is also growing disenchantment with the role of hatcheries in reversing the decline of commercially valuable salmonid stocks, or in helping with the restoration of threatened salmon populations (Levin, Zabel & Williams, 2001). Supportive breeding has become one of the most widely used strategies for managing declining salmonids all over the world (Cowx, 1998), despite increasing concerns that releasing large numbers of 'maladapted' individuals may hinder, rather than help, the recovery of threatened natural populations (e.g. Levin *et al.*, 2001; Levin & Williams, 2002; Ford, 2002). Clearly, there has never been a more urgent time to address the study of adaptive variation of a rapidly dwindling resource.

Here we critically review the scale and extent of adaptive variation in Atlantic salmon and examine the wider implications of local adaptations for conservation and management. Although we have largely focused our attention on *Salmo salar*, and on those papers published since Taylor's (1991) review, reference has also been made to other salmonids and other fish species where appropriate.

### (1) What is adaptive variation?

Adaptive genetic variation has been variously defined as 'heritable phenotypic variation that is sorted by natural selection into different environmental niches, so enhancing

fitness in specific environments' (Robinson & Schluter, 2000; Carvalho *et al.*, 2003), but also as 'genetic variation that is correlated with fitness' (Endler, 2000). Thus adaptive variation can be examined from a phenotypic or genotypic perspective (see Reeve & Sherman, 1993) and linking these two (the genotype-phenotype problem: West-Eberhard, 2003) is possibly one of the greatest challenges in evolutionary ecology (Purugganan & Gibson, 2003; Bernatchez, 2004). With this in mind, we use here the term *adaptive genetic variation* to include both heritable variation in fitness-related phenotypic traits and adaptive variation at the molecular level.

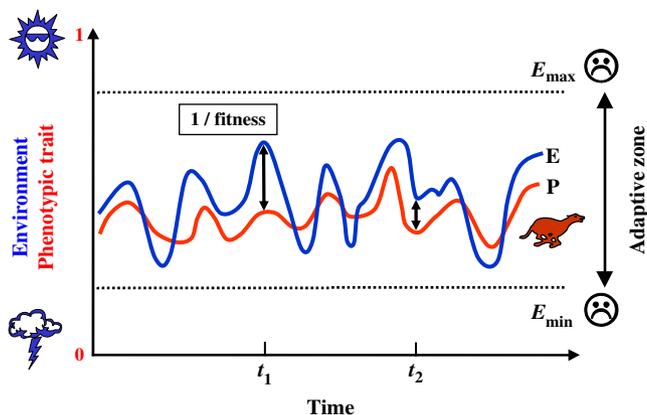
The above definitions highlight three obvious, but important, points:

(1) natural selection cannot generate genetic variation *per se*, but is the only evolutionary force that can result in adaptations, (2) not all genetic variation is adaptive, and (3) not all phenotypic variation is inherited. They also stress the fact that adaptive variation is essentially context-specific, for it enhances fitness (*i.e.* is adaptive) in some environments but not in others. More specifically, under some conditions, divergent selection may result in local adaptations, manifested by the superior performance of local individuals compared to immigrants (Lenormand, 2002; but see Kawecki & Ebert, 2004 for other criteria for local adaptations). Thus, the existence of genetic variation for phenotypic traits (a requisite), adaptive variation (an outcome), and local adaptations (a process) are not the same thing.

Similarly, it is important to distinguish between *inheritance*, which indicates simply that a phenotypic trait is under genetic control, and *narrow sense heritability* (or simply *heritability*,  $h^2$ ), which indicates the proportion of phenotypic variability accounted for by variation in additive genetic variance, or in other words, the extent to which individuals resemble their parents (Houle, 1992). Thus, the possession of an adipose fin is a heritable trait in salmonids, but it has a heritability of zero since there is no variation among individuals within this family. Information on heritabilities (discussed later) is important in studies of adaptive variation because (1) the higher the heritability, the greater (faster) the response to selection is likely to be (Mazer & Damuth, 2001), but also because (2) under constant environmental conditions, traits under strong selection (*i.e.* closely related to fitness) should have low heritabilities (Falconer & MacKay, 1996), since advantageous alleles would tend to become fixed (but see Endler, 2000).

### (2) How are adaptations generated and maintained?

If environments did not vary in space and time, organisms would eventually become quite well adapted at living in them: those phenotypes that performed well in the past should do well in the future and successful phenotypes would converge towards one, or perhaps a few 'all-round, winning designs'. Real environments, however, are neither constant, nor are they perfectly predictable, so organisms are forever struggling to keep pace with environmental change (Fig. 1). There is never a single phenotype that can outperform the others under all environmental conditions (Moran, 1992), and frequency-dependence (a common



**Fig. 1.** Temporal changes in fitness in changing environments (see text for explanations). Adaptation can be defined as the good fit of organisms to their environment (Gould & Lewontin, 1979; Meyers & Bull, 2002), and can be seen as the process of change in response to natural selection (Reznick & Travis, 2001). At any given time how well adapted an organism is depends on both its phenotype (P) and the current environmental conditions (E). Fitness can be viewed as the degree of matching between the two, and natural selection can be thought of as a greyhound always attempting to track environmental change. However, since the environment is not constant, and natural selection can only act on yesterday's designs, phenotypes are likely to be maladapted to some extent (i.e. natural selection is always 'late'). The better the phenotype matches the environment, the fitter the population (or organism) might be expected to be. In the example illustrated here the population might be expected to perform "better" (i.e. has a higher mean fitness) at time  $t_2$  than at time  $t_1$  since there is a better matching between the two (i.e. the vertical distance is smaller). Although both the environment (E) and the phenotype (P) can range widely for a given species, a population is subjected to only a small subset of possible environmental conditions and displays a relatively narrow range of possible phenotypes. Together these define an 'adaptive zone' of ontogenetic variation (*sensu* Mazer & Damuth, 2001), contained between  $E_{\max}$  (the upper environmental limit) and  $E_{\min}$  (the lower environmental limit) which represents all the non-zero fitness points in the 'adaptive landscape' (*sensu* Schluter, 2000) defined by the relationship between trait values and fitness.

phenomenon in nature) makes it possible for several phenotypes to coexist in an evolutionarily stable state (Maynard Smith, 1982). Phenotypic diversity is therefore the norm. Further, since natural selection can only act on yesterday's designs, most phenotypes are bound to be maladapted to some extent.

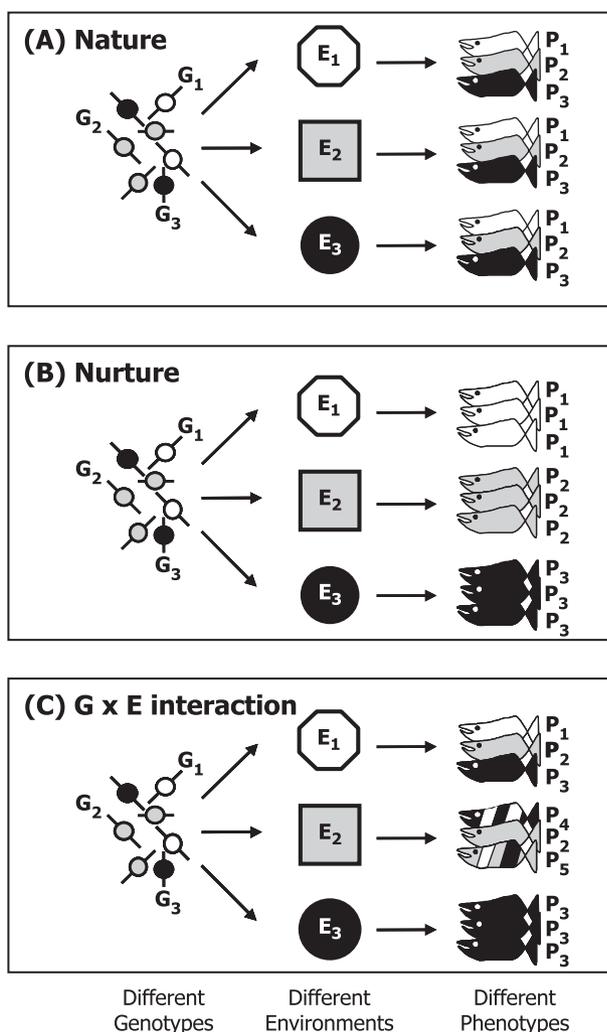
However, how do genotypes produce phenotypes of varying plasticity to adapt to environmental change, and what roles do the environment and the genes play in shaping salmonid populations? This is, of course, another way of restating the old nature (the genes) *versus* nurture (the environment) debate: are the differences we observe among salmon populations simply the result of having different genes (the nature hypothesis), or are they the result of living in different environments (the nurture hypothesis)? The answer, of course, is both. As Ricker's (1972) seminal work

on Pacific salmon (*Oncorhynchus* sp.) put it decades ago (p. 146): "...the evidence available at hand is now quite considerable. It indicates that most of the studied differences between local stocks can and usually do have both a genetic and an environmental basis".

The phenotype we observe represents the interaction of a set of genes with a range of environmental conditions. Therefore, phenotypic variation can arise from three fundamentally different ways: from purely genetic effects, from purely environmental effects, and from the interaction between genes and the environment (Fig. 2). A fourth source of phenotypic variation – developmental instability – can also be the target of selection (Lajus, Graham & Kozhara, 2003). However, it is the existence of genotype-by-environment interactions for some traits in Atlantic salmon that provides the best insight into the nature of adaptive divergence (Fig. 2). Such interactions (antagonistic pleiotropy: Kawecki & Ebert, 2004) suggest that different genotypes may be optimal in different environments (although not all  $G \times E$  interactions need be adaptive in salmonids: Hutchings, 2004).

In the absence of other evolutionary forces, spatial heterogeneity and divergent selection (selection that increases the difference between alternative phenotypes, West-Eberhard, 2003) should cause populations to be adapted to their local environments. However, other microevolutionary forces such as gene flow and genetic drift may promote or constrain adaptive divergence (Kawecki & Ebert, 2004), particularly in the case of small populations (Kimura & Ohta, 1971). Theory predicts that gene flow should impose an upper limit on local adaptation (Lenormand, 2002), but the extent of the constraint is open to debate (Storfer, 1999; Saint-Laurent, Legault & Bernatchez, 2003; Hendry & Taylor, 2004). Adaptive divergence seems to be negatively correlated with gene flow in many species (see examples in Mousseau, Sinervo & Endler, 2000 and Dieckmann *et al.*, 2004), but the strength of this association is variable because (a) divergent selection can differ substantially between traits, and (b) there is a large amount of unexplained variance implying that factors other than gene flow and selection are also important in determining adaptive divergence (Hendry & Taylor, 2004). For example, phenotypic plasticity may slow down or speed up population differentiation (Price, Qvarnström & Irwin, 2003), while fine-scale environmental heterogeneity coupled with non-random dispersal may reinforce, rather than counteract, adaptive divergence (Garant *et al.*, 2005).

Genetic drift (random loss of alleles) can cause random (non-adaptive) genetic differentiation of salmonid populations, even in cases where divergent selection would tend to favour the development of local adaptations (Adkison, 1995; Hensleigh & Hendry, 1998). This is because when populations are very small, genetic drift may cause weakly selected genes to start behaving like neutral genes, and natural selection to become less effective (Primack, 1998). Because the strength of natural selection depends on the effective population size ( $N_e$ ), rather than on the actual size of the population ( $N$ ), populations that have grown from a few founder individuals (founder effect) or that experience



**Fig. 2.** Nature, nurture and the development of local adaptations. Phenotypic differences between Atlantic salmon populations (*i.e.* those we can observe, represented by fish of different patterns) can arise in three fundamentally different ways: (A) from purely genetic effects, (B) from purely environmental effects, or (C) from genotype-by-environment interactions. A fourth source of phenotypic variation - developmental instability - has been recognized recently (see review by Lajus *et al.*, 2003). In a purely genetic scenario (A) phenotypic variation is solely the result of genetic variation, *i.e.* different genotypes ( $G_1$ – $G_3$ ) will always produce certain phenotypes ( $P_1$ – $P_3$ ) regardless of the environment where they live (the nature hypothesis). In this case, what may appear to be local adaptations are merely the result of different sets of genes, for example due to founder effects or genetic drift (e.g. Adkison, 1995). By contrast, in a purely environmental scenario (B), habitat heterogeneity is the only diversifying agent responsible for making populations the way they are. Thus, what may appear to be locally adapted phenotypes ( $P_1$ – $P_3$ ) are merely the result of habitat heterogeneity (the nurture hypothesis). In the third scenario (C) different genotypes interact with the environment in different ways to produce an array of different phenotypes ( $P_1$ – $P_3$ ). Local adaptations are more likely to occur here since there is not a single genotype which is best in all environments. Hence, local adaptations can be viewed as evolutionarily important forms of  $G \times E$  interactions (Myers *et al.*, 2001; Kawecki & Ebert, 2004). Traits for which there is evidence of  $G \times E$  interactions in Atlantic salmon include age at maturity, body size, growth efficiency, growth rate, muscle growth, survival, and resistance to sea lice infections, amongst others (see Table 2).

sunfish *Lepomis gibbosus* – Robinson & Schluter, 2000; see also Hendry, 2004).

### (3) How are adaptations detected?

There are many different ways to test for the effects of natural selection and detect the existence of adaptations (Endler, 1986; Rose & Lauder, 1996; Mousseau *et al.*, 2000; Reznick & Travis, 2001). However, while almost any feature can be shown to be adaptive (the spandrels of San Marco paradigm: Gould & Lewontin, 1979), it is virtually impossible to prove that a property of an organism has no selective value (Mayr, 2002). Consequently, many studies claiming demonstration of local adaptations failed to actually do so, and were rightly criticised for making these claims (Gould & Lewontin, 1979).

Because of the complexity of influences, Reznick & Travis (1996, 2001) argued that the most effective way to establish cause and effect is to examine the evolutionary dynamics of adaptations rather than simply trying to interpret the adaptive significance of a trait (see also Schluter, 2000). To do so, one observes the patterns in nature and attempts to devise complementary studies of contemporary dynamics (we cannot repeat history) that can uncover the extent to which these patterns have been moulded by adaptive evolution. Multiple perspectives will provide the most compelling cases for adaptation, combining the observation

strong reductions in abundance (bottlenecks) may be particularly susceptible to genetic drift (Primack, 1998). There are few estimates of effective population sizes in natural salmon populations, but those available indicate that the effective size may be less than 10% of the census size in Atlantic salmon (Consuegra *et al.*, 2005d) and other salmonids (Shrimpton & Heath, 2003; Waples, 2004, 2005). Thus, even relatively large populations are at risk of losing rare alleles and, at least theoretically, capable of producing random differentiation within the context of single populations (Adkison, 1995). However, within the context of metapopulations, genetic drift may promote rather than inhibit local adaptations by converting non-additive genetic variation into additive genetic variation, upon which selection can act (Mazer & Damuth, 2001). Field studies have shown that even in small founding populations, rapid evolution driven by natural selection (Reznick, Rodd & Nunney, 2004) can be the main diversifying agent in salmonids (Quinn, Unwin & Kinnison, 2000; Hendry *et al.*, 2000; Koskinen, Haugen & Primmer, 2002; Consuegra *et al.*, 2005c), as well as in other fish species (e.g. guppies *Poecilia reticulata* - Reznick *et al.*, 1997; Reznick & Ghalambor, 2001; three-spined stickleback *Gasterosteus aculeatus*, pumpkinseed

Table 1. Methodological approaches employed to study adaptive genetic variation in Atlantic salmon and their relative utility (+, ++) for uncovering the existence of local adaptations. Asterisks indicate studies on other salmonids

Methodological approach	Genetic basis of trait divergence	Selection on specific traits	Specific agents of selection	Local adaptations (local <i>versus</i> foreign criterion) <sup>1</sup>	Local adaptations (home <i>versus</i> away criterion) <sup>2</sup>	Example
1. Clines and ecological correlates		+	+			Claytor <i>et al.</i> (1991) Jordan <i>et al.</i> (2005)
2. Genetic differences among families or populations in adaptive traits	++					Riddell <i>et al.</i> (1981) Garant <i>et al.</i> (2002, 2003b)
3. Translocations	+	+		+	+	Garcia de Leaniz <i>et al.</i> (1989) Crozier <i>et al.</i> (1997)
4. Common-garden Experiments	++	+		+		McGinnity <i>et al.</i> (2003) McGinnity <i>et al.</i> (2004)
5. Reciprocal transplants	++	++		++	++	Mayama <i>et al.</i> (1989)*
6. Mark recapture of individuals with different traits		++				Hendry <i>et al.</i> (2003) Garcia de Leaniz <i>et al.</i> (2000)
7. Experimental manipulation of traits		++	+			Einum & Fleming (2000a,b) Hendry <i>et al.</i> (2004b)*
8. Experimental manipulation of selective agents		+	++			Pakkasmaa & Piironen (2001a,b) Jonsson <i>et al.</i> (2001)
9. QTL/genomics	++	++				Aubin-Horth <i>et al.</i> (2005) Perry <i>et al.</i> (2005)*

<sup>1</sup>Local *versus* foreign criterion for local adaptations: in each habitat, local fish perform better than immigrants from other habitats.

<sup>2</sup>Home *versus* away criterion for local adaptations: local fish perform better in their own habitat (home) than in other habitats (away).

QTL, quantitative trait loci.

Common-garden experiment: different populations are reared in a common environment in an attempt to dissociate heritable from environmentally induced phenotypic variation.

of patterns (a static approach) with experimental studies (a dynamic approach). Different complementary approaches have been used to study adaptations in salmonids (Table 1), which vary in their ability to uncover the nature and extent of adaptive variation (see Endler, 1986, 2000).

First, comparative studies can help to establish a relationship between the phenotype (trait) and specific features of the environment (ecological correlates), providing clues to the potential adaptive significance of the trait(s) and, in the case of clines, perhaps also on the specific agents of selection (Table 1). Such comparisons can be made spatially, among populations, and/or temporally, within populations across time. This has been by far the most common approach employed to study adaptive variation in salmonids (Table 2), although it has limited or no power to uncover the existence of local adaptations (Table 1).

Building on comparative studies, breeding studies serve to demonstrate that the trait variation under study has a genetic basis. This has commonly been achieved by breeding experiments under communal conditions (Tables 1,2), although several generations of rearing may be needed to control for non-genetic maternal effects (Falconer & MacKay, 1996). However, demonstration of genetic variation for a trait within a single population is not

sufficient to demonstrate that the variation among populations has a genetic basis. That is, the demonstration of heritability *sensu strictu* is neither necessary nor a sufficient condition for studying the adaptive significance of trait variation among populations (Reznick & Travis, 1996).

A third, more powerful method for studying adaptive variation is to carry out reciprocal transplant experiments, whereby phenotypic variation can be partitioned into effects attributable to local environment, population of origin, and the interaction of population and environment. Such reciprocal transfers can generally help to uncover (e.g. Linhart & Grant, 1996) or rule out (e.g. van Nouhuys & Via, 1999) the existence of local adaptations (Table 1), though there may not always be conclusive evidence (e.g. Brown *et al.*, 2001). Unfortunately, very few reciprocal transfers seem to have been carried out with salmonids (Mayama *et al.*, 1989), and none that we know of involving Atlantic salmon. On the other hand, results of translocations and common-garden field experiments (where different populations are raised in a common environment in an attempt to dissociate heritable from environmentally induced phenotypic variation) involving native and foreign populations have provided useful insights into adaptive variation in salmon (Table 2), but may have limited value to uncover

Table 2. Evidence for heritable variation in fitness-related phenotypic traits among and within populations of Atlantic salmon. Asterisks indicate studies suggesting genotype-by-environment interactions. 'Environment' refers to the testing conditions (W, wild releases; L, laboratory or cage conditions; S, semi-natural channel), 'Stage' refers to the freshwater (F) and marine (M) stages of salmon development, and 'Method' refers to the primary approach or method(s) used to detect genetic variation in phenotypic traits (1: comparative ecological correlates; 2: genetic differences among families or populations; 3: translocations/common-garden experiments; 4: mark-recapture of individuals with different traits; 5: experimental manipulation of traits; 6: QST method, QTL, genomics; see text)

Dependent trait	Environment	Stage	Method	Reference
<b>Among populations</b>				
Body size* <sup>a</sup>	W	M	2	Jonasson <i>et al.</i> (1997)
Body size	L	F	2	Jonasson (1993)
Body morphology	L	F	1,2	Riddell <i>et al.</i> (1981)
Body morphology	L/S	F	2	Fleming & Einum (1997)
Growth rate	L	F	2	Holm & Fernö (1986)
Growth rate	L	F	2	Nicieza <i>et al.</i> (1994b)
Growth rate	L	F	2	Torrissen <i>et al.</i> (1993)
Growth rate	W	M	2	Friedland <i>et al.</i> (1996)
Growth rate	L/W	F	2,3	McGinnity <i>et al.</i> (1997)
Growth rate	L/W	F & M	2,3	McGinnity <i>et al.</i> (2003)
Growth rate* <sup>a</sup>	L	M	2	Gunnes & Gjedrem (1978)
Growth rate* <sup>b</sup>	L	F	1,2	Jonsson <i>et al.</i> (2001)
Growth rate	L/W	F	2	Einum & Fleming (1997)
Growth rate	L/S	F	2	Fleming & Einum (1997)
Growth efficiency* <sup>b</sup>	L	F	1,2	Jonsson <i>et al.</i> (2001)
Muscle growth* <sup>b</sup>	L	F	1,2	Johnston <i>et al.</i> , (2000b,c)
Muscle growth	L	F	1,2	Johnston <i>et al.</i> , (2000a)
Digestive rate	L	F	2	Nicieza <i>et al.</i> (1994a)
Embryo development	L	F	2	Berg & Moen (1999)
Survival	L/W	F	2,3	McGinnity <i>et al.</i> (1997)
Survival	L/W	F & M	2,3	McGinnity <i>et al.</i> (2003)
Survival	L	F	2	Jonasson (1993)
Survival	W	F & M	2	Garcia de Leaniz <i>et al.</i> (1989)
Survival	W	F & M	2	Verspoor & Garcia de Leaniz (1997)
Survival	W	M	1	Friedland <i>et al.</i> (1996)
Survival	W	M	3	Hansen & Jonsson (1990)
Survival* <sup>a</sup>	W	M	3	Jonasson (1996)
Survival* <sup>a</sup>	W	M	2	Jonasson <i>et al.</i> (1997)
Survival* <sup>c</sup>	L	F	2	Gjedrem & Aulstad (1974)
Survival* <sup>d</sup>	L/W	F	2,3	Donaghy & Verspoor (1997)
Survival* <sup>d</sup>	L	F & M	1,2	Rosseland <i>et al.</i> (2001)
<i>Gyrodactylus</i> resistance	L	F	1,2	Bakke <i>et al.</i> (1990), Bakke (1991)
Age at sexual maturity	W	M	2,3	McGinnity <i>et al.</i> (2003)
Age at sexual maturity	L	M	1,2	Nævdal <i>et al.</i> (1978)
Age at sexual maturity	L/W	M	3	Jonasson (1996)
Age at sexual maturity*	L	M	1,2	Glebe & Saunders (1986)
Age at sexual maturity	L	M	2	Holm & Nævdal (1978)
Male parr maturation*	L	F	1,2	Glebe & Saunders (1986)
Marine migrations	W	M	1,2,4	Kallio-Nyberg & Koljonen (1999)
Marine migrations	W	M	1,2,4	Kallio-Nyberg <i>et al.</i> (1999)
Smolt migration timing	W	F	2	Aarestrup <i>et al.</i> (1999)
Smolt migration timing	W	F	2,3	Nielsen <i>et al.</i> (2001)
Smolt migration timing	W	F	2	Orciari & Leonard (1996)
Timing of hatching*	L/W	F	2,3	Donaghy & Verspoor (1997)
Seasonal run-timing	W	M	3	Hansen & Jonsson (1991)
Seasonal run-timing	W	M	2,3	Stewart <i>et al.</i> (2002)
Sheltering behaviour	L	F	1,2	Valdimarsson <i>et al.</i> (2000)
Aggression levels	L	F	1,2	Holm & Fernö (1986)
Aggression levels*	L	F	2,3	Einum & Fleming (1997)
Predator avoidance	L	F	2,3	Einum & Fleming (1997)
Aggression levels*	L/S	F	3	Fleming & Einum (1997)
Predator avoidance	L/S	F	3	Fleming & Einum (1997)
Predator avoidance	L	F	1,2	Jonsson <i>et al.</i> (2001)
<b>Within populations</b>				
Body size	L	M	2	Gjedrem (1979)

Table 2. (cont.)

Dependent trait	Environment	Stage	Method	Reference
Body size	L	M	2	Nævdal (1983)
Body size	L	M	2	Friars <i>et al.</i> (1990)
Body size	L	M	2	Rye & Refstie (1995)
Body size*	W	F	2	Garant <i>et al.</i> (2003a)
Body size	W	F	4	Hendry <i>et al.</i> (2003)
Condition factor	W	F	4	Hendry <i>et al.</i> (2003)
Egg size	S,W	F	4,5	Einum & Fleming (2000a,b)
Egg size	L	F	2	Pakkasmaa <i>et al.</i> (2001)
Growth rate	L	F	2	Thorpe & Morgan (1978)
Growth rate	L	F & M	2	Gjerde (1986)
Growth rate	L	M	2	Friars <i>et al.</i> (1990)
Growth rate	L	F	2	Rye <i>et al.</i> (1990)
Growth rate	L	F	2	Torrissen <i>et al.</i> (1993)
Growth rate	L	F	2	Thodesen <i>et al.</i> (2001a)
Growth rate*	W	F	2,5	Garant <i>et al.</i> (2003a)
Growth rate	W	F	4	Hendry <i>et al.</i> (2003)
Growth efficiency	L	F	2	Thodesen <i>et al.</i> (2001a)
Feeding rate	L	F	2	Thodesen <i>et al.</i> (2001a)
Embryo development	L	F	2	Berg & Moen (1999)
Date of emergence	S,W	F	4,5	Einum & Fleming (2000a,b)
Date of emergence	W	F	4	Garcia de Leaniz <i>et al.</i> (2000)
Length at emergence	S,W	F	4,5	Einum & Fleming (2000a,b)
Alevin length	W	F	4	Garcia de Leaniz <i>et al.</i> (2000)
Marine migrations	W	M	2,4	Kallio-Nyberg <i>et al.</i> (2000)
Marine migrations	W	M	2,4	Jutala <i>et al.</i> (2003)
Survival	L	F	2	Rye <i>et al.</i> (1990)
Survival	L	F	2	Thorpe & Morgan (1978)
Survival* <sup>c</sup>	L	F	2	Fevolden <i>et al.</i> (1993, 1994)
Survival* <sup>c</sup>	L	F	2	Gjedrem & Gjøen (1995)
Survival* <sup>c</sup>	L	F	2	Langefors <i>et al.</i> (2001)
Survival* <sup>c</sup>	L	F	2	Lund <i>et al.</i> (1995)
Survival* <sup>c</sup>	L	M	2	Bailey <i>et al.</i> (1993)
Survival* <sup>c</sup>	L	M	2	Standal & Gjerde (1987)
Survival* <sup>d</sup>	L	F	2	Schom (1986)
Survival* <sup>e</sup>	L	F	2	Gjøen <i>et al.</i> (1997)
Early survival	W	F	4	Garcia de Leaniz <i>et al.</i> (2000)
Stress	L	F	2	Fevolden <i>et al.</i> (1991)
Sea louse infection*	L	M	2	Mustafa & MacKinnon (1999)
Age at sexual maturity	L	M	2	Nævdal (1983)
Age at sexual maturity	L	M	2	Gjerde (1984)
Age at sexual maturity*	L/W	F	6	Aubin-Horth <i>et al.</i> (2005)
Muscle growth	L	F	2	Johnston <i>et al.</i> (2000b)
Reproductive success	W	F	2,5	Garant <i>et al.</i> (2003a)

<sup>a</sup> Differences in relative performance among rearing/release locations.

<sup>b</sup> differences in relative performance among different temperatures.

<sup>c</sup> differences in resistance to diseases.

<sup>d</sup> differences in tolerance to low pH levels.

<sup>e</sup> negative genetic correlation between resistance to viral and bacterial diseases.

QTL, quantitative trait loci.

QST method, extent of population differentiation in quantitative traits ( $Q_{ST}$ ) presumed to be affected by selection relative to neutral molecular markers ( $F_{ST}$ ).

local adaptations (Table 1) due to post-release stress and maternal effects (Kawecki & Ebert, 2004).

Mark-recapture studies allow quantification of mortality rates and lifetime reproductive success associated with individuals exhibiting particular traits of interest. This makes it possible to generate detailed information about the dynamics of natural selection, as done, for example, in Galapagos finches (Grant & Grant, 2002) or North American red squirrels *Tamiasciurus hudsonicus* (Réale *et al.*,

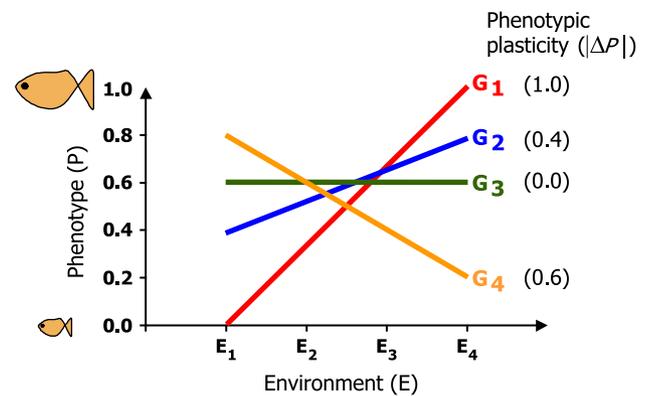
2003), and also recently on Atlantic salmon (Hendry, Letcher & Gries, 2003; Table 2).

A fifth complementary approach to studying adaptation involves experimental manipulation of a population to allow a more direct evaluation of a trait to fitness (e.g. Sinervo & Licht, 1991; Schluter, 1994, 2000). This can help to test hypotheses about the effects of selection on specific traits (Table 1) and provide clues on the specific agents of selection (e.g. on oxygen and egg size in Atlantic salmon – Einum,

Thorstad & Næsje, 2002; on reproductive trade-offs and senescence in sockeye salmon *Oncorhynchus nerka* - Hendry *et al.*, 2004b).

A further approach to the study of adaptive variation has been made possible by recently developed methods in quantitative genetics and in genomics. These can be used to detect selection on specific traits (Table 1), and to examine the nature and significance of adaptive variation in natural populations (reviewed in Vasemägi & Primmer, 2005). Two popular quantitative approaches involve examining the  $Q_{ST}/F_{ST}$  ratio (the  $Q_{ST}$  method; Merilä & Crnokrak, 2001), and the direction of effects of quantitative trait loci for specific traits (the QTL method; McKay & Latta, 2002). The  $Q_{ST}$  method compares the extent of population differentiation in quantitative traits ( $Q_{ST}$ ) and in neutral molecular markers ( $F_{ST}$ ). In the absence of selection, differences between populations are expected to be solely due to mutation and random genetic drift, so populations should tend to differ as much in their phenotype as they do in neutral markers (*i.e.*  $Q_{ST} = F_{ST}$  under the neutral expectation). Adaptive differentiation, on the other hand, can be inferred when populations differ more in quantitative phenotypic traits than they do in allelic frequencies (*i.e.*  $Q_{ST} > F_{ST}$ ), provided gene flow is low, genetic variance in quantitative traits is purely additive, and there are no genotype by environment interactions (Schluter, 2000). In practice, phenotypic variance is commonly used as a proxy of additive genetic variance, which is typically unknown in natural populations (Bernatchez, 2004). The stronger the local adaptation, the more  $Q_{ST}$  will tend to differ from  $F_{ST}$  (McKay & Latta, 2002), particularly when population divergence is not too old and  $F_{ST}$  is still relatively low (Schluter, 2000; Hendry, 2002). Similarly, when population differentiation is lower for quantitative traits than it is for neutral molecular markers (*i.e.*  $Q_{ST} < F_{ST}$ ), this may be indicative of balancing (rather than divergent) selection (Schluter, 2000; Bernatchez, 2004). With the QTL method, directional selection can be inferred when a suite of QTL effects vary consistently in the same direction, whereas the trait is likely to have evolved under neutrality when QTL exhibit opposing effects (Rieseberg *et al.*, 2002).

While  $Q_{ST}$  and QTL approaches hold considerable scope for examining phenotypic diversification in fishes (Bernatchez, 2004), only genomic technologies offer the potential for identifying those genes directly affected by natural selection, and for examining how these are expressed under different selective pressures (Oleksiak, Churchill & Crawford, 2002; Luikart *et al.*, 2003). There are large, ongoing QTL mapping projects in farmed salmonids (e.g. Fjalestad, Moen & Gomez-Raya, 2003; Moen *et al.*, 2004) examining fitness-related traits such as body size (O'Malley *et al.*, 2003; Perry *et al.*, 2005), spawning date (O'Malley *et al.*, 2003), disease resistance (Moen *et al.*, 2004) or thermal performance (Somorjai, Danzmann & Ferguson, 2003; Perry *et al.*, 2005), and these will undoubtedly facilitate the study of adaptive differentiation and local adaptations in these species. However, because different classes of gene will likely experience different selective pressures, the ultimate promise of molecular genomics is a general theory of adaptation linking genetic variation with phenotypic varia-



**Fig. 3.** Reaction norms of different genotypes with different degrees of phenotypic plasticity. The concepts of phenotypic plasticity (DeWitt *et al.*, 1998; Price *et al.*, 2003) and genotype-by-environment interaction (Mazer & Damuth, 2001) help to resolve the nature *versus* nurture debate (see Pigliucci, 2001) and provide a plausible mechanism for the development of local adaptations. Phenotypic plasticity is said to occur whenever the phenotype ( $P$ , 0–1) produced by a given genotype ( $G_1$ – $G_4$ ) depends on the environment ( $E_1$ – $E_4$ ). The phenotypic trajectory that describes a given genotype in a range of environmental conditions is termed the “reaction norm” (see Hutchings, 2004 for the application of reaction norms to the study of salmonid life histories). For a given genotype, reaction norms, thus, may be said to “translate” environmental variation into phenotypic variation (Mazer & Damuth, 2001). The hypothetical example shown here depicts the phenotypes that could result when salmon with different genotypes ( $G_1$  to  $G_4$ ) are reared in an environmental gradient ( $E_1$  to  $E_4$ ). In this case, the four reaction norms converge to similar phenotypes at intermediate environments ( $E_2$  and  $E_3$ ), but produce diverging phenotypes at the environmental extremes ( $E_1$  and  $E_4$ ), revealing the existence of genotype-by-environment interactions. Note that phenotypic plasticity differs between genotypes, being very high for  $G_1$  (1.0), intermediate for  $G_4$  (0.6), and low for  $G_2$  (0.4). The phenotype produced by  $G_3$  may be said to be purely genetic (*i.e.* plasticity is 0) as the same phenotype is obtained in all environments. The other three (plastic) genotypes, on the other hand, could give rise to local adaptations.

tion (Purugganan & Gibson, 2003). In this respect, the complete mapping and sequencing of the Atlantic salmon genome with the aid of molecular genomics (Rise *et al.*, 2004; Thorsen *et al.*, 2005) should be a major turning point in the study of adaptive evolution in this and related species.

Demonstrating local adaptations of single traits following all required criteria may be considered somewhat of an academic enterprise. Fortunately, in terms of importance for management and conservation, it all boils down to whether - for a given environment - native individuals are better suited and perform better than foreign individuals. Yet, even such a seemingly easy question remains to be answered for all but a few of the world's species. Thus, for most organisms, including Atlantic salmon, the extent, importance and spatial scale of adaptive variation can only be inferred from knowledge of the key factors: natural selection, spatial environmental variation, interactions between selection and environmental factors (*i.e.* genotype-by-environment

interactions; see Figs 2 and 3), effective population sizes, and the extent of gene-flow among populations.

## II. EXTENT OF ADAPTIVE VARIATION IN ATLANTIC SALMON

In Atlantic salmon, as in all organisms, adaptive variation comes in three classes: (1) there is phenotypic variation in important, fitness-related traits, (2) there is genetic variation at the molecular level in non-neutral genes, influenced by selection, and (3) there is variation in the way the genes interact with the environment to produce phenotypes of varying plasticity. In each case, to be regarded as adaptive, we must show that such variation meets two conditions: (a) that trait differences among populations are inherited (the trait may be inherited but shows no genetic variation among populations) and (b) that such variation makes local populations perform better in their home environment than in foreign ones (local *versus* foreign criterion), or perform better in their home environment than in other environments (home *versus* away criterion: Kawecki & Ebert, 2004).

### (1) Heritable variation in fitness-related phenotypic traits

Many morphological, life-history, and behavioural traits show significant heritable variation both within and among Atlantic salmon populations (Table 2); these translate into differences in survival and fitness in both freshwater and marine stages, and are thus likely to be adaptive (even though, it must be stressed, the fitness implications are inferred and not directly demonstrated). Furthermore, since many of these studies also indicate the existence of genotype-by-environment interactions, different genotypes seem to be optimal in different environments, creating conditions for local adaptations to develop (Kawecki & Ebert, 2004).

#### (a) Body morphology and meristics

As in other salmonids (e.g. Ricker, 1972; Quinn, 2005), natural populations of Atlantic salmon can differ greatly with respect to meristic and morphometric characters (Riddell & Leggett, 1981; Kazakov, 1998), and many such morphological differences have been inferred to be adaptive (see Taylor, 1991, for a review of the early literature). For example, Claytor, MacCrimmon & Gots (1991) analysed 47 wild Atlantic salmon populations located throughout the species' range in North America and Western Europe and found that fish with longer heads and more streamlined bodies tended to predominate in high-gradient rivers with higher water velocities, as had been indicated in previous studies (Riddell & Leggett, 1981; Riddell, Leggett & Saunders, 1981). Common-garden breeding experiments confirmed that such morphological variation was heritable, for differences among Atlantic salmon populations persisted when fish were reared under the same environment (Riddell *et al.*, 1981). A relationship between water velocity and

body shape is also evident in other salmonids (Taylor & MacPhail, 1985; Taylor, 1991), and may represent an adaptive response to water flow. Indeed, juvenile salmonids experimentally reared in fast flowing waters differ in shape from juveniles reared under low flows, and the degree of phenotypic plasticity appears to be high (Pakkasmaa & Piironen, 2001*b*). Thus, morphological variation in juvenile salmonids - either as a result of genetic variation or phenotypic plasticity - is thought to represent an adaptation to local environmental conditions (Riddell *et al.*, 1981; Pakkasmaa & Piironen, 2001*a,b*). Then, as juveniles begin to smolt, their morphologies seem to converge in preparation for a shift to the more homogeneous marine environment (Nicieza, 1995; Letcher, 2003). Later, when spawners return to freshwater to breed, variation in adult body morphology and secondary sexual traits may increase again (e.g. Naesje, Hansen & Järvi, 1988; Witten & Hall, 2003) and have important fitness implications (e.g. Järvi, 1990; Fleming, 1996; Fleming & Reynolds, 2004).

Thus, Atlantic salmon seem to show heritable variation in body morphology, as can be inferred from experimental crosses (Table 2) and significant heritability estimates (e.g. body condition factor - Table 3); furthermore, since body morphology (or some correlated trait) has a direct effect on performance (Table 4) and reproductive success (Table 5), at least some of the observed morphological variation must be of adaptive value.

#### (b) Life-history traits

Variation in life-history traits is also considerable in Atlantic salmon (Gardner, 1976; Thorpe & Stradmeyer, 1995) and other salmonids (Ricker, 1972; Hendry & Stearns, 2004; Quinn, 2005). Quantitative life-history traits that are important for fitness include age and size at maturity, reproductive investment (including egg size), age- and size-specific survival, and longevity (Stearns, 1992). Not only do these traits differ among Atlantic salmon populations (N. Jonsson, Hansen & Jonsson, 1991; Hutchings & Jones, 1998; L'Abée-Lund, Vøllestad & Beldring, 2004), they also vary within populations (Jonsson, Jonsson & Fleming, 1996; Fleming, 1998; Good *et al.*, 2001; Table 2). For example, variation in age at maturity may range from a few months for mature male parr at the southern end of the range to 10 or more years for large anadromous fish at the northern extreme (reviewed by Gardner, 1976; Hutchings & Jones, 1998). Different age classes give rise to different phenotypes, that differ in body size, behaviour, sex ratio, and reproductive success (see Meerburg, 1986). Thus, mature male parr may weigh 1,000 times less than anadromous males, and also differ in the pattern of energy allocation, life-history traits, and fertilisation success (Thomaz, Beall & Burke, 1997; Whalen & Parrish, 1999; Ardnt, 2000; Taggart *et al.*, 2001; Garant *et al.*, 2002; Letcher & Gries, 2003).

Laboratory and field studies indicate that variation in many life-history traits, including body size, male parr maturation, smolt age, and age at maturity is heritable in Atlantic salmon (Tables 2 & 3). For example, Nævdal *et al.* (1978) noted a relationship between age at maturity in sea

Table 3. Heritability estimates ( $h^2_s$ ) for various fitness-related traits in Atlantic salmon computed from the sire component of variance or mixed-model analysis; number (n), range, mean values, and standard deviations (S.D.) of heritability estimates are indicated. 'Stage' refers to freshwater (F) or marine (M) stages. 'Env' refers to artificial (A) or natural (N) conditions

Trait	Stage	Env	Heritability estimate ( $h^2_s$ )			References	
			n	Range	Mean		S.D.
<b>Size, growth &amp; physiology</b>							
Fillet colouration/carotenoid concentration	M	A	7	0.01–0.60	0.31	0.22	Gjerde & Gjedrem (1984) Rye & Storebakken (1993) Rye & Gjerde (1996) Refstie <i>et al.</i> (1996)
Body length (cm)	M	A	8	0.08–0.42	0.23	0.13	Gunnes & Gjedrem (1978) Refstie & Steine (1978) Gjerde & Gjedrem (1984) Standal & Gjerde (1987) Jonasson (1993) Rye & Refstie (1995)
Body length (cm)	F	A	4	0.15–0.57	0.38	0.21	Nævdal <i>et al.</i> (1975)
Body mass (g)	F	A	4	0.08–0.32	0.19	0.12	Refstie & Steine (1978) Bailey <i>et al.</i> (1991) Jonasson (1993) Gjerde <i>et al.</i> (1994)
Body weight (g or kg)	M	A	20	0.05–0.44	0.25	0.13	Gunnes & Gjedrem (1978) Gjerde & Gjedrem (1984) Standal & Gjerde (1987) Gjerde <i>et al.</i> (1994) Rye & Refstie (1995) Jonasson & Gjedrem (1997) Rye & Mao (1998) <sup>2</sup>
Body mass (kg), ranched 1SW	M	N	3	0.20–0.36	0.26	0.09	Jonasson (1995) Jonasson & Gjedrem (1997)
Body mass (kg), ranched 2SW	M	N	1	–	0.00 <sup>NS</sup>	–	Jonasson (1995)
Condition factor	M	A	5	0.05–0.37	0.23	0.15	Standal & Gjerde (1987) Rye & Refstie (1995) Rye & Gjerde (1996)
Specific growth rate (% body mass day <sup>-1</sup> )	M	A	5	0.04–0.26	0.14	0.10	Gjerde <i>et al.</i> (1994)
Fat content (% or score)	M	A	5	0.09–0.35	0.25	0.10	Rye & Gjerde (1996) Refstie <i>et al.</i> (1996)
Slaughter yield (%)	M	A	2	0.03–0.20	0.12	0.12	Gjerde & Gjedrem (1984) Rye & Gjerde (1996)
Belly flap thickness (score)	M	A	1	–	0.16	–	Gjerde & Gjedrem (1984)
Swimming stamina			1	–	0.24	–	Hurley & Schom (1984)
Daily feed intake (%body mass day <sup>-1</sup> )	F	A	1	–	+	–	Thodesen <i>et al.</i> (2001a)
Thermal growth coefficient	F	A	1	–	+	–	Thodesen <i>et al.</i> (2001a)
Feed efficiency ratio	F	A	1	–	+	–	Thodesen <i>et al.</i> (2001a)
Amino acid absorption	F	A	1	–	+	–	Thodesen <i>et al.</i> (1999)
Mineral absorption	F	A	1	–	+	–	Thodesen <i>et al.</i> (1999)
Mineral absorption	M	A	1	–	+	–	Thodesen <i>et al.</i> (2001b)
<b>Life-history &amp; survival</b>							
Age at smolting	F	A	1	–	+	–	Bailey & Friars (1990)
Age at maturity (% 1SW)	M	A	6	0.04–0.16	0.10	0.05	Gjerde (1986) Gjerde <i>et al.</i> (1994) Wild <i>et al.</i> (1994)
Age at maturity (% 1SW) ranched	M	N	1	–	0.65 <sup>1</sup>	–	Jonasson (unpublished data)
Age at maturity (% 2SW)	M	A	3	0.08–0.17	0.13	0.05	Standal & Gjerde (1987) Gjerde <i>et al.</i> (1994)
Survival (% eyed ova)	F	A	1	–	0.29 <sup>1</sup>	–	Rye <i>et al.</i> (1990) <sup>1</sup>
Survival (% alevin or fry)	F	A	5	0.09–0.29	0.13 <sup>1</sup>	0.09	Rye <i>et al.</i> (1990) Jonasson (1993)
Return rate (%), ranched 1SW	M	N	1	–	0.12 <sup>2</sup>	–	Jonasson (1995)

Table 3. (cont.)

Trait	Stage	Env	Heritability estimate ( $h^2_s$ )			S.D.	References
			n	Range	Mean		
Return rate (%), ranches 2SW	M	N	1	–	0.08 <sup>2</sup>	–	Jonasson (1995)
<b>Resistance to diseases &amp; parasites</b>							
Furunculosis (antibody titre or % survival)	F/M	A	7	0.02–0.53	0.28	0.19	Gjedrem <i>et al.</i> (1991 <i>b</i> ) Bailey <i>et al.</i> (1993) Strømsheim <i>et al.</i> (1994 <i>a</i> ) Gjedrem & Gjøen (1995) <sup>NS</sup> Lund <i>et al.</i> (1995) <sup>NS</sup> Gjøen <i>et al.</i> (1997) <sup>1</sup>
CW vibriosis (antibody titre or % survival)	F/M	A	7	0.00–0.19	0.09	0.06	Standal & Gjerde (1987) Strømsheim <i>et al.</i> (1994 <i>b</i> ) <sup>NS</sup> Lund <i>et al.</i> (1995) Gjedrem & Gjøen (1995) <sup>NS</sup> Fjalestad <i>et al.</i> (1996) <sup>NS</sup>
Vibriosis (antibody titre or % survival)	F/M	A	5	0.01–0.69	0.21	0.28	Gjedrem & Aulstad (1974) Strømsheim <i>et al.</i> (1994 <i>b</i> ) Fjalestad <i>et al.</i> (1996) <sup>NS</sup> Gjøen <i>et al.</i> (1997) <sup>1</sup>
BKD (% survival)	M	A	2	–	0.23	–	Gjedrem & Gjøen (1995) Anon (1996)
ISA (% survival)	F	A	1	–	0.19	–	Gjøen <i>et al.</i> (1997) <sup>1</sup>
<i>Diphtheria</i> toxoid (antibody titre)	M	A	1	–	0.09	–	Eide <i>et al.</i> (1994)
Salmon lice (number of sea lice)	M	A	1	–	0.19	–	Salte (unpublished data)
<b>Health condition</b>							
Total haemolytic activity (% standard)	F	A	2	0.04–0.35	0.20	0.22	Røed <i>et al.</i> (1992) Fevolden <i>et al.</i> (1994) <sup>NS</sup>
Non-specific haemolytic activity (% standard)	F	A	3	0.02–0.32	0.19	0.15	Røed <i>et al.</i> (1992) Røed <i>et al.</i> (1993) <sup>NS</sup> Fevolden <i>et al.</i> (1994) <sup>NS</sup>
Lysozyme activity (% standard)	F/M	A	3	0.08–0.19	0.14 <sup>NS</sup>	0.06	Røed <i>et al.</i> (1993) Fevolden <i>et al.</i> (1994) Lund <i>et al.</i> (1995)
Total immunoglobulins (IgM, g l <sup>-1</sup> or titre)	M	A	2	0.00–0.12	0.06	0.08	Strømsheim <i>et al.</i> (1994 <i>b</i> ) Lund <i>et al.</i> (1995) <sup>NS</sup>
Post-stress cortisol level (ng ml <sup>-1</sup> )	F	A	2	0.05–0.07	0.06 <sup>NS</sup>	0.01	Fevolden <i>et al.</i> (1993) Fevolden <i>et al.</i> (1994)
RBC cell membrane fragility	F	A	1	–	0.60	–	Gjedrem <i>et al.</i> (1991 <i>a</i> )
Specific haemolytic activity (% standard)	F	A	1	–	0.29	–	Røed <i>et al.</i> (1992)
Spinal deformities (%)	F	A	1	–	0.25	–	McKay & Gjerde (1986)
$\alpha_2$ -antiplasmin level (% human ref.)	M	A	1	–	0.19	–	Salte <i>et al.</i> (1993)
$\alpha_2$ -macroglobulin level (% human ref.)	M	A	1	–	0.12 <sup>NS</sup>	–	Salte <i>et al.</i> (1993)
Fibrinogen level (% human ref.)	M	A	1	–	0.11 <sup>NS</sup>	–	Salte <i>et al.</i> (1993)
$\alpha_1$ -antiproteinase level (% human ref.)	M	A	1	–	0.10 <sup>NS</sup>	–	Salte <i>et al.</i> (1993)
Post-stress glucose (mg ml <sup>-1</sup> )	F	A	1	–	0.03 <sup>NS</sup>	–	Fevolden <i>et al.</i> (1993)
Antithrombin (% human ref.)	M	A	1	–	0.03 <sup>NS</sup>	–	Salte <i>et al.</i> (1993)
Serum iron concentration ( $\mu$ g ml <sup>-1</sup> )	F	A	1	–	+	–	Ravndal <i>et al.</i> (1994)

+ : significant variation between full- and/or half-sib groups.

<sup>NS</sup> Heritability estimate does not differ significantly from zero.

<sup>1</sup>Heritability estimates for binary traits computed on the underlying liability scale.

<sup>2</sup>Excluding effects due to dominance, additive x additive epistasis and common environment.

SW, seawinter; CW, coldwater; BKD, bacterial kidney disease; ISA, infectious salmon anaemia; RBC, red blood cell.

cages and age at maturity in the wild source populations. Differences among wild populations in the incidence of grilse (*i.e.* salmon that mature after only one winter at sea) were maintained when fish were raised in a common environment, suggesting a genetic basis for age at maturity (see also L'Abée-Lund *et al.*, 2004). In sea ranching, the

heritability for grilse rate can be as high as 0.65 (Jonasson, unpublished data). Holm and Nævdal (1978) estimated heritability for age at maturity of different stocks and ages of Atlantic salmon to be between 0.05 and 0.10, while the mean estimate from different studies was found to be 0.10 for grilse and 0.13 for two sea-winter salmon (Table 3).

Table 4. Evidence for the influence of behaviour, morphology, and physiology on performance of Atlantic salmon. 'Conditions' refer to conditions of the study and 'Stage' to freshwater (F) and marine (M) stages of the species

Independent phenotypic/ genetic trait	Dependent performance trait	Direction	Conditions	Stage	Reference
<b>Behaviour</b>					
Aggression	growth rate	— <sup>a</sup>	laboratory	F	Holm & Fernö (1986)
Dominance	growth rate	+	laboratory	F	Metcalfe <i>et al.</i> (1992)
Dominance	growth rate	+	semi-natural	F	Huntingford <i>et al.</i> (1998)
Dominance	growth rate	+	semi-natural	F	O'Connor <i>et al.</i> (2000)
Dominance	growth rate	—	semi-natural	F	Huntingford & Garcia de Leaniz (1997)
Dominance	growth rate	0	wild release	F	Martin-Smith & Armstrong (2002)
Dominance	settlement	—	semi-natural	F	Huntingford & Garcia de Leaniz (1997)
Emergence time <sup>b</sup>	growth rate	—	laboratory	F	Metcalfe & Thorpe (1992)
Emergence time <sup>c</sup>	body size	—	wild release	F	Einum & Fleming (2000b)
Emergence time <sup>c</sup>	survival	—	wild release	F	Einum & Fleming (2000b)
Movement rates	growth rate	—	semi-natural	F	Huntingford <i>et al.</i> (1998)
Movement rates	growth rate	+	wild release	F	Martin-Smith & Armstrong (2002)
Prior residency	growth rate	+	semi-natural	F	O'Connor <i>et al.</i> (2000)
Prior residency	growth rate	+	semi-natural	F	Huntingford & Garcia de Leaniz (1997)
Prior residency	settlement	+	semi-natural	F	Huntingford & Garcia de Leaniz (1997)
Timing of emergence	settlement	+	wild	F	Garcia de Leaniz <i>et al.</i> (2000)
Timing of smolt release	survival	<sup>d</sup>	wild release	M	Hansen & Jonsson (1989)
Timing of smolt release	survival	<sup>e</sup>	wild release	M	Staurnes <i>et al.</i> (1993)
Timing of smolt release	survival	<sup>f</sup>	wild release	M	Eriksson (1994)
<b>Morphology &amp; physiology</b>					
Allozyme heterozygosity	growth efficiency	+	laboratory	F	Blanco <i>et al.</i> (2001)
Allozyme heterozygosity	growth rate	+	laboratory	F	Blanco <i>et al.</i> (1998)
Allozyme heterozygosity	growth rate	+	laboratory	F	Blanco <i>et al.</i> (2001)
MEP-2* (100) allele	body size	+	wild	M	Consuegra <i>et al.</i> (2005a)
MEP-2* (100) allele	body size	+	wild	M	Morán <i>et al.</i> (1994, 1998)
MEP-2* (100) allele	body size	+/—	wild	F	Gilbey <i>et al.</i> (1999)
MEP-2* (100) allele	growth rate	+/—	wild	F	Jordan & Youngson (1992)
MEP-2* (100) allele	body size	—	wild	F	Jordan & Youngson (1991)
MEP-2* (100) allele	male parr maturation	—	wild	F	Jordan & Youngson (1991)
MEP-2* (100) allele	age at maturity	+	wild	M	Consuegra <i>et al.</i> (2005a)
MEP-2* (100) allele	age at maturity	+	wild	M	Morán <i>et al.</i> (1994, 1998)
MEP-2* (100) allele	age at maturity	+	wild	M	Jordan <i>et al.</i> (1990)
Body size	survival	+	wild release	F	Einum & Fleming (2000a)
Body size	survival	+	laboratory	F	Meekan <i>et al.</i> (1998)
Body size	survival	+/— <sup>g</sup>	wild	F	Good <i>et al.</i> (2001)
Body size	survival	+	wild	F	Jensen & Johnsen (1984)
Body size	survival	+	wild release	F	Einum & Fleming (2000b)
Body size	survival	+	wild release	M	Farmer (1994)
Body size	survival	+	wild release	M	Lundqvist <i>et al.</i> (1988)
Body size	survival	+	wild release	M	Salminen & Kuikka (1995)
Body size	survival	+	wild release	M	Vehanen <i>et al.</i> (1993)
Body size	survival	+	wild release	M	Eriksson (1994)
Egg size	body size	+	laboratory	F	Kazakov (1981)
Egg size	body size	+	wild release	F	Einum & Fleming (2000a)
Egg size	survival	+	wild release	F	Einum & Fleming (2000a)
Egg size	survival	+ <sup>h</sup>	laboratory	F	Einum <i>et al.</i> (2002)
Egg carotenoid levels	hatching success	0	laboratory	F	Christiansen & Torrissen (1997)
Energetic content	survival	+	wild	F	Gardiner & Geddes (1980)
Fluctuating asymmetry	survival	—	wild release	F	Morán <i>et al.</i> (1997)
Fluctuating asymmetry	stress	+/—	laboratory	F	Vøllestad & Hindar (1997)

<sup>a</sup> Comparison among populations. One highly aggressive population showed slower growth than two other populations.

<sup>b</sup> Variation within a single family.

<sup>c</sup> Variation among families.

<sup>d</sup> Survival highest for smolt released at normal time for smoltification in the particular river.

<sup>e</sup> Survival correlated with temporal changes in seawater tolerance.

<sup>f</sup> Survival increased throughout season.

<sup>g</sup> Selection for large fry during drought year, selection for small fry during flood year.

<sup>h</sup> Under low levels of dissolved oxygen.

MEP-2\*, malic enzyme.

Table 5. Evidence for the influence of behaviour, morphology and physiology on traits associated with reproductive success of Atlantic salmon. 'Conditions' refers to whether the work was conducted in experimental (E) or natural river environments (N) and 'Scale' refers to level of analysis, *i.e.* nest (N, individual spawning events), redd (R, groups of nests of a single female) or population (P). 'Stage' refers to male parr (MP), anadromous males (AM) and anadromous females (AF)

Independent trait	Dependent Trait	Direction	Conditions	Scale	Stage	Reference
Body size	0+ offspring	+	N	P	AM & AF	Garant <i>et al.</i> (2001)
Body size	aggression, spawnings, surviving embryos	+	E	P	AM & AF	Fleming <i>et al.</i> (1996)
Body size	aggression, spawnings, surviving embryos	+	E	P	AM & AF	Fleming (1998)
Body size	embryos	+	N	N	MP	Garant <i>et al.</i> (2002)
Body size	eyed embryos	+	E	R	MP	Thomaz <i>et al.</i> (1997)
Body size	eyed embryos	+	E	R	MP	Jones & Hutchings (2001)
Body size	eyed embryos	0	E	N & P	MP	Jones & Hutchings (2002)
Body size	eyed embryos	0	E	N & P	AM	Jones & Hutchings (2002)
Body size	paternity	+	E	N	AM	Mjølnerød <i>et al.</i> (1998)
Body size	spawnings, surviving embryos	+	E	P	AM & AF	Fleming <i>et al.</i> (1997)
Body size	dominance	+	E	P	AM	Järvi (1990)
Kype size	dominance	+	E	P	AM	Järvi (1990)
Adipose fin size	dominance	+	E	P	AM	Järvi (1990)
Dominance	matings	+	E	P	AM	Järvi (1990)
MHC	0+ offspring	disassortative	N	P	AM & AF	Landry <i>et al.</i> (2001)
Number of mates	0+ offspring	+	N	P	AM & AF	Garant <i>et al.</i> (2001)

MHC, major histocompatibility complex.

Average heritabilities for body length were 0.23 in sea rearing (range 0.08–0.42) and 0.38 in freshwater culture (range 0.15–0.57; Table 3). Although some of these estimates are lower than the average heritability (0.268) for life-history traits across several animal groups, they do indicate the existence of genetic variation for body size and age at maturity in salmon (Weigensberg & Roff, 1996). However, it is not clear to what extent heritabilities obtained in artificial conditions are applicable to the field (e.g. Hoffmann, 2000), or what is the extent of phenotypic plasticity for life-history traits in Atlantic salmon. For example, Reimers, Kjørrefjord & Stavøstrand (1993) manipulated age at maturity by altering ration levels in the preceding winter, while Saunders *et al.* (1983) and Friedland, Haas & Sheehan (1996) found significant differences in grilse rates between artificial and natural conditions that could be attributed to the different environment and sea-growth experienced by post-smolts (L'Abée-Lund *et al.*, 2004). Similarly, in coho (*Oncorhynchus kisutch*) and chinook (*O. tshawytscha*) salmon, early male maturity is influenced both by body size attained in fresh water prior to seaward migration and by growth rate at sea, emphasising the importance of phenotypic plasticity in the life-history traits of salmonids (Vøllestad, Peterson & Quinn, 2004).

Mature male parr and grilse tend to father more mature parr than multi-sea winter males when crossed with the same females, suggesting that there is a heritable basis for early sexual maturation (Glebe & Saunders, 1986). However, the expression of early maturation in male parr may depend as much on its genes as on attaining a certain body size or growth threshold during development (Prévost, Chadwick & Claytor, 1992; Hutchings & Myers, 1994; Gross, 1996; Whalen &

Parrish, 1999; Aubin-Horth & Dodson, 2004). Within such 'conditional strategy', then, each male has the capability of becoming sexually mature as parr, and it is the size threshold for maturation (or some other measure of condition, e.g. energy at a given time) that appears to be heritable (and variable) among individuals and populations (Hutchings & Myers, 1994; Aubin-Horth & Dodson, 2004).

Taken together, these studies suggest significant phenotypic plasticity for life-history traits in Atlantic salmon - and genetic variation for reaction norms among individuals and populations (Fig. 3) - probably resulting from differences in physiological trade-offs (Aubin-Horth & Dodson, 2004; Vøllestad *et al.*, 2004). Of all phenotypic traits, variation in body size (or in underlying characters such as smolt age or age at maturity) appears to be particularly influential on both fitness components (Table 4) and reproductive success (Table 5).

### (c) Development rates and event timing

Atlantic salmon populations can differ greatly in developmental rates and in the timing of key, life-history events, and these were once thought to give rise to different populations or 'races' (Calderwood, 1908; Huntsman, 1937; Berg, 1959). While environmental cues (in particular water temperature and photoperiod) seem to account for much of the observed variation in developmental rates and the onset of migratory (McCormick *et al.*, 1998; Björnsson *et al.*, 2000; Riley, Eagle & Ives, 2002; Byrne *et al.*, 2003) and reproductive behaviour (Fleming, 1996, 1998), there is also increasing evidence for genetic variation in the timing of life-history events (Table 2). Thus, in addition to inherited differences in seasonal migration timing (Hansen & Jonsson,

1991; Stewart, Smith & Youngson, 2002), Atlantic salmon populations also seem to exhibit heritable variation in breeding time (Heggberget, 1988; Fleming, 1996; Webb & McLay, 1996), in the timing of hatching and emergence (Donaghy & Verspoor, 1997; Berg & Moen, 1999), in the timing and pattern of smolt migration (Riddell & Leggett, 1981; Orciari & Leonard, 1996; Nielsen *et al.*, 2001), and in the spatio-temporal distribution of adults at sea (Kallio-Nyberg, Koljonen & Saloniemi, 2000).

Variation in the timing of many life-history events is not only inherited, it can also have important implications for fitness (Table 4). For example, delayed alevin emergence has a negative effect on alevin growth rate (Metcalf & Thorpe, 1992), alevin size (Einum & Fleming, 2000*b*) and survival (Einum & Fleming, 2000*b*), whereas prior residency resulting from early emergence generally leads to enhanced growth rates (Huntingford & Garcia de Leaniz, 1997; O'Connor, Metcalfe & Taylor, 2000; Letcher *et al.*, 2004), and advantages in territorial disputes (Huntingford & Garcia de Leaniz, 1997; Harwood *et al.*, 2003; Metcalfe, Valdimarsson & Morgan, 2003). Similarly, variation in the timing of spawning (Heggberget, 1988; Fleming, 1996; Webb & McLay, 1996; Mjølnerød *et al.*, 1998) or in the timing of smolt migration (Hansen & Jonsson, 1989; Staurnes *et al.*, 1993; Eriksson, 1994) can affect survival, and are therefore likely to be the targets of natural selection.

#### (d) Physiology and thermal optima

Although thermal tolerance is thought to be relatively constant across salmonid populations (Elliott, 1994), upper lethal temperatures in Atlantic salmon can vary by as much as 3°C among individuals (Garside, 1973; Elliott, 1991). Water temperature represents one of the most conspicuous environmental differences among Atlantic salmon rivers (Elliott *et al.*, 1998), and varies latitudinally and seasonally in a predictable way that promotes the development of local adaptations. Thermal performance, thus, may be expected to vary among populations though there are few comparative studies or heritability estimates. Optimal temperatures for juvenile growth have been reported to vary between 15 and 20°C (Elliott & Hurley, 1997; Jonsson *et al.*, 2001) with an upper threshold for normal feeding at approximately 22°C (Elliott, 1991), and a cessation of growth normally below 4–7°C (Thorpe *et al.*, 1989; Jonsson *et al.*, 2001).

Among wild populations living in complex environments, water temperature and growth may not be correlated because seasonally variable energy intake is partitioned in a temperature-dependent manner between assimilation (growth) and maintenance costs (Jones *et al.*, 2002; Bacon *et al.*, 2005). Thus, if selection acts on thermal performance, including growth, it may act indirectly through temperature-dependent behavioural traits related to food acquisition or metabolic efficiency. For example, many behavioural traits such as overwintering sheltering (Rimmer, Saunders & Paim, 1985; Cunjak 1988), smolt migration (Rimmer & Paim, 1990; Erkinaro, Julkunen & Niemelä, 1998; Byrne *et al.*, 2003) or spawning activity (Fleming, 1996; de Gaudemar & Beall, 1999) are modulated by temperature

in Atlantic salmon, and can thus be the targets of temperature-related selection.

Comparison of populations from the Rivers Shin (Scotland) and Narcea (Spain) showed that under common environmental conditions, northern fish grew faster in summer and autumn while those from the southern population grew fastest in winter and spring (Nicieza, Reyes-Gavilán & Braña, 1994*b*). As growth opportunities in northern Atlantic salmon populations are greatest in summer and autumn, an adaptive response to feeding opportunity seems likely. A difference in digestive performance was suggested as a possible mechanism for producing growth rate differences (Nicieza, Reiriz & Braña, 1994*a*). Digestive performance was higher in northern fish at a range of temperatures (5, 12 and 20°C), with the difference being greatest at high temperatures, suggesting that the genotypes of the northern population can efficiently exploit feeding opportunities across a wide range of thermal conditions (Nicieza *et al.*, 1994*a*). Indeed, variation in both thermal growth coefficients and feeding rates appear to be inherited (Thodesen *et al.*, 2001*a*).

In another study, Jonsson *et al.* (2001) studied five Norwegian populations under a range of temperatures, and found significant differences among populations in the optimal temperatures for both growth rate and growth efficiency. There did not seem to be any correlation between thermal optima and thermal conditions in the rivers from which the populations originated. However, maximum growth efficiencies were greatest in those populations with the lowest opportunities for feeding and growth, suggesting again a possible adaptive advantage. Similarly, water temperature seems to have different effects on muscle growth of early- and late-maturing populations (Johnston *et al.*, 2000*a,b,c*), apparently in relation to their natal river temperatures. Such geographic variation in genotypes that counteracts environmental influences along a gradient, often maintaining phenotypic similarity, is termed 'counter-gradient variation' (Conover & Schulz, 1995).

Many other physiological and biochemical traits are heritable in Atlantic salmon (Tables 2–3), including response to stress (Fevolden, Refstie & Røed, 1991), carotenoid levels (perhaps related to sexual selection - Gjerde & Gjedrem, 1984; Rye & Storebakken, 1993; Rye & Gjerde, 1996; Refstie *et al.*, 1996), specific growth rate (Gjerde, Simianer & Refstie, 1994), fat content (Rye & Gjerde, 1996; Refstie *et al.*, 1996), swimming stamina (Hurley & Schom, 1984), and absorption of amino acids and minerals (Thodesen *et al.*, 1999, 2001*b*).

#### (e) Behaviour

It is often assumed that there is a connection between the nature of a character and the magnitude of its heritability. Characters with the lowest heritability should be those most closely associated with fitness (Falconer & Mackay, 1996), a prediction often upheld by empirical studies (Mousseau & Roff, 1987; Merilä & Sheldon, 1999). Behavioural traits are assumed to be closely related to fitness, and following Fisher's fundamental theorem, additive genetic variance should be low for alleles directly regulating fitness (Merilä &

Sheldon, 1999; Stirling, Réale & Roff, 2002). However, recent studies indicate that the heritability of behavioural traits is low mainly due to a high residual variance, rather than due to a low additive genetic variance (Merilä & Sheldon, 1999; Stirling *et al.*, 2002), which may result in local adaptations if directional selection is strong enough. Indeed, behavioural traits closely related to fitness and subject to strong genotype-by-environment interactions will tend to have lower heritabilities (Mazer & Damuth, 2001), and higher genetic and non-genetic variability (Houle, 1992) than characters under weak selection. However, there are very few field estimates of heritability values for behavioural traits in natural animal populations, as most studies have been conducted in laboratory or farm conditions (Stirling *et al.*, 2002). This is unfortunate, since heritability estimates can differ greatly between environments (Weigensberg & Roff, 1996) and it may not always be possible to extrapolate from the laboratory to the wild (Hoffman, 2000).

For Atlantic salmon, few - if any - heritability estimates are available for behavioural traits. However, there are a number of studies showing that variation in some important behavioural traits probably has a genetic basis. Studies can be grouped into three broad categories: (1) comparisons among families and populations, (2) comparison between wild and hatchery fish, and (3) comparisons between normal and transgenic individuals.

Few studies have clearly documented inherited differences in behaviour between natural Atlantic salmon populations. Some exceptions (Table 2) include heritable variation in sheltering behaviour (e.g. Valdimarsson, Metcalfe & Skúlason, 2000) and aggression levels (Holm & Fernö, 1986) between populations. Other studies (e.g. Aarestrup *et al.*, 1999) have also documented significant differences in smolt movement and migration patterns of populations released in a novel environment. Taken together, these studies indicate that inherited variation in behavioural traits such as aggression, sheltering, or pattern of migration all have the potential to result in local adaptations, either due to directional selection on the traits themselves or on other, correlated traits.

Individuals and populations may also differ in their choice of habitats. Indeed, the possibility that salmon with different genotypes may differ in their preferred habitat optima has important implications for conservation and management, for example in the development of habitat quality guidelines or in the assessment of environmental impacts. However, despite extensive work on habitat preferences of Atlantic salmon in streams (e.g. Whalen, Parrish & Mather, 1999; Nislow, Folt & Parrish, 2000; Heggenes *et al.*, 2002) and on genetic structuring of populations on larger scales (e.g. Fontaine *et al.*, 1997; McConnell *et al.*, 1998; Garant, Dodson & Bernatchez, 2000), very little is known about potential interactions between local habitat and genetic variation. The variety of salmon habitats certainly provides the opportunity for variation in habitat selection among genotypes but few studies have addressed this question in the field. Based on a single sampling of fry stocked as eggs in a stream, Webb *et al.* (2001) found variation in density among families and

habitats but no interaction between family and habitat. These results suggest that family differences in density can exist but that families may respond to habitat variation in similar ways (*i.e.* no genotype-by-environment interaction). However, more studies are clearly needed to address this question. Similarly, although co-operative social behaviour towards kin has been demonstrated in Atlantic salmon under semi-natural conditions (Brown & Brown, 1993, 1996; Griffiths & Armstrong, 2000, 2002), the high dispersal rates in streams, the relatively low densities, and the presence of half-sibs, make kin-biased behaviour less likely to occur in the field (Fontaine & Dodson, 1999; but see Carlsson & Carlsson, 2002 and Olsén *et al.*, 2004 for recent field studies).

Many studies have investigated domestication and examined the genetic basis of behavioural differences between wild and hatchery-reared individuals. However, many of these studies are difficult to interpret, as there are often several, alternative explanations for the observed differences in behaviour. For example, wild and hatchery fish do not normally experience the same environment during early life. This means that any possible genetic effects may be confounded by differences in early history (maternal effects, environmental effects), since it may be impossible to disentangle the effects of phenotypic plasticity (differences in reaction norms) from the additive genetic effects. This is the case for a number of telemetry studies showing differences in migratory behaviour between farmed and wild salmon (B. Jonsson, Jonsson & Hansen, 1991; Heggberget, Økland & Ugedal, 1993, 1996; Økland, Heggberget & Jonsson, 1995; Thorstad, Heggberget & Økland, 1998), and tagging studies showing differences in smolt migratory behaviour (B. Jonsson *et al.*, 1991). Even detailed experimental studies showing differences in reproductive behaviour and spawning success of farmed and wild salmon (e.g. Fleming *et al.*, 1996) may be confounded in the same way (but see Fleming *et al.*, 2000).

Despite the above difficulties, some studies do indicate that at least some behavioural differences between farmed and wild salmon are inherited, and are likely to be adaptive. For example, comparisons of a seventh-generation strain of farmed salmon with its principal founder population indicate a strong genetically-based change in aggression level and predator avoidance behaviour (Fleming & Einum, 1997; Johnsson, Höjesjö & Fleming, 2001). Further, in a common-garden field study (McGinnity *et al.*, 2003), juvenile farm salmon and farm × wild hybrids outcompeted wild fish in fresh water, but showed poor survival at sea and reduced overall life-time success when compared to the wild population. Thus, artificial selection resulting from domestication may be strong enough to produce significant differences in behaviour in a few generations. However, neither the heritability of the traits affected by domestication, nor the selection intensity experienced by domesticated salmon are known.

Recent studies on transgenic salmonids also suggest that certain differences in behavioural traits must be inherited. For example, salmon genetically modified with a growth hormone transgene display significantly higher movement and consumption rates than controls in the face of risk of

predation (Abrahams & Sutterlin, 1999). Moreover, when confronted with danger, control fish (without the transgene) avoid the high-risk area whereas growth-enhanced transgenic fish continue to feed at high rates and sustain high predation rates (Sundström *et al.*, 2004). These results suggest that hormonal controls over growth rate and behaviour are linked, although the genetic architecture (level of genetic and environmental variance, genetic correlations) of such traits remains unclear.

#### (f) Health condition and resistance to parasites and diseases

Variation in health and natural resistance to pathogens has been extensively studied in Atlantic salmon, owing to its importance to the salmon farming industry (Table 3). Health traits for which significant heritability estimates have been obtained include variation in several blood parameters and incidence of spinal deformities, amongst others (Table 3). Resistance to other important diseases such as furunculosis, vibriosis, cold-water vibriosis, bacterial kidney disease (BKD), infectious salmon anemia (ISA), and *Diphtheria* toxoid is also inherited, with mean heritability estimates across studies ranging between 0.09 and 0.28 (Table 3).

The geographical pattern of inherited resistance to the monogenean parasite *Gyrodactylus salaris* constitutes probably the most convincing example of adaptive variation leading to local adaptation in Atlantic salmon. Unlike Baltic populations, which are generally resistant to infection by *Gyrodactylus salaris*, salmon populations migrating into the Atlantic are generally susceptible or partially susceptible to the parasite (Bakke, 1991; Bakke, Jansen & Hansen, 1990; Bakke & MacKenzie, 1993; Rintamäki-Kinnunen & Valtonen, 1996; Bakke, Harris & Cable, 2002; Dalgaard, Nielsen & Buchmann, 2003). The comparative phylogenies of Atlantic salmon (Verspooor *et al.*, 1999; Nilsson *et al.*, 2001; Consuegra *et al.*, 2002) and *Gyrodactylus salaris* (Meinilä *et al.*, 2004) suggest that *G. salaris* was originally a parasite of the European grayling (*Thymallus thymallus*) in the Baltic during the last Ice Age, and that Baltic salmon gradually acquired resistance through prolonged contact while salmon from the Atlantic basin did not.

## (2) Adaptive variation in non-neutral, selected genes

Atlantic salmon display a significant degree of population structuring with genetic variation distributed hierarchically among four levels: (1) among three major groupings (western Atlantic, eastern Atlantic and Baltic), (2) among lineages within each grouping (e.g. northern and southern lineages within the Baltic), (3) among river systems, and (4) among tributaries within river systems. Thus, strong homing behaviour (reviewed by Stabell, 1984) results in significant genetic differences not only between major groupings separated thousands of kilometres, but also among populations inhabiting nearby tributaries of major river systems, only a short distance apart (e.g. Fontaine *et al.*, 1997; Spidle *et al.*, 2001; Verspooor *et al.*, 2002). However, only genetic variation that has an effect on fitness (*i.e.* is non-neutral) can

have adaptive value. Unfortunately, while knowledge of levels and patterns of neutral genetic variation in Atlantic salmon is well developed (e.g. King *et al.*, 2000, 2001; Consuegra *et al.*, 2002; Spidle *et al.*, 2001, 2003), there is relatively little information on the adaptive significance of non-neutral, selected markers. This comes mostly from studies that have examined genetic correlates on three types of markers: (1) isozymes, (2) major histocompatibility complex (MHC), and (3) mitochondrial DNA.

#### (a) Isozymes

The existence of clines in the distribution of non-neutral genetic variants (typically allozymes) along environmental gradients may indicate the effect of selection (e.g. Powers, 1990; Powers *et al.*, 1991). Several allozyme polymorphisms in Atlantic salmon appear to be non-neutral (e.g. Torrissen, Male & Nævdal, 1993; Torrissen, Lied & Espe, 1994, 1995; Verspooor, 1986, 1994; Verspooor *et al.*, 2005), but it is perhaps the malic enzyme locus (*MEP-2\**) that provides the best circumstantial evidence in support of selection. Atlantic salmon populations inhabiting warm rivers tend to show high frequencies of the *MEP-2\* 100* allele, whereas populations living in cold rivers tend to show high frequencies of the alternative (*\*125*) allele, thereby forming a latitudinal cline in both Europe and North America (Verspooor & Jordan, 1989). Moreover, significant differences in *MEP-2\** frequencies also exist among populations within river systems (Verspooor & Jordan, 1989; Verspooor, Fraser & Youngson, 1991), and these seem to be maintained by natural selection (Verspooor *et al.*, 1991; Jordan, Verspooor & Youngson, 1997), apparently in relation to juvenile growth (Jordan & Youngson, 1991; Gilbey, Verspooor & Summers, 1999) and age at maturity (Jordan, Youngson & Webb, 1990; Consuegra *et al.*, 2005a).

This suggests that genetic variation at the malic enzyme locus - or at some tightly linked gene(s) - is probably adaptive and that the observed differences between salmon populations may reflect local adaptations to different thermal regimes. Nevertheless, some uncertainty still remains and, as in the case of other protein polymorphisms in fish (e.g. *Fundulus heteroclitus*, Powers *et al.* 1991; sea bass *Dicentrarchus labrax* Allegrucci *et al.*, 1994), direct experimental evidence is probably needed to rule out alternative explanations (e.g. gene 'hitch-hiking') and to clarify the adaptive role of malic enzyme on Atlantic salmon.

#### (b) Major histocompatibility complex (MHC) genes

A central component of the immune system in vertebrates, MHC genes are involved in the recognition of pathogens and initiation of the immune response. They are the most polymorphic genes in the vertebrate genome and this high level of variability is thought to be a product of natural selection for the ability to respond to a wide range of pathogens: *i.e.* individuals that are heterozygous at MHC loci can recognise and respond to a wider range of infectious disease organisms than homozygous individuals. MHC genotype has been associated with a range of fitness-related traits in a variety of species and MHC genes

currently represent the best system available in vertebrates to study how natural selection can promote local adaptations (Bernatchez & Landry, 2003).

The MHC genes of the Atlantic salmon are only now beginning to be examined in any detail (Grimholt *et al.*, 2002, 2003; Stet *et al.*, 2002; Consuegra *et al.*, 2005*b,c*). However, challenge experiments have already shown associations between specific MHC alleles and resistance or susceptibility to bacterial (furunculosis, causative agent: *Aeromonas salmonicida*) and viral (ISA, causative agent: infectious salmon anaemia virus) diseases (Langefors *et al.*, 2001; Lohm *et al.*, 2002; Grimholt *et al.*, 2003). The Atlantic salmon is one of the few species in which convincing evidence of specific MHC/disease relationships has been demonstrated. In addition, when levels of differentiation at MHC genes are examined and compared to those at selectively neutral microsatellite loci, MHC genes generally show higher levels of differentiation, suggesting that spatial heterogeneity in selective pressures on MHC genes in Atlantic salmon promotes local adaptation, with the effect most pronounced in a within-river comparison (Landry & Bernatchez, 2001; Consuegra *et al.*, 2005*c*; Langefors, 2005). Selection for MHC variability in offspring may also explain the evidence for preference for mates with a different MHC genotype seen in Atlantic salmon (Landry *et al.*, 2001).

#### (c) Mitochondrial DNA (mtDNA)

Variation in maternally-inherited mitochondrial DNA (mtDNA) is typically assumed to be neutral to selection (Avice, 1994), though some evidence suggests that this may not always be the case (Ballard & Kreitman, 1995; Hey, 1997). For example, in Atlantic salmon historical changes in mtDNA variation may be associated with post-glacial warming (Consuegra *et al.*, 2002), and with differential fishing pressure exerted by anglers on distinct population components (Consuegra *et al.*, 2005*a*). Experimental studies are clearly needed to examine the possible adaptive significance of the extensive mtDNA variation detected across the species range (Verspoor *et al.*, 1999, 2002; King *et al.*, 2000; Nilsson *et al.*, 2001; Asplund *et al.*, 2004; Tonteri *et al.*, 2005).

The recent detection in Atlantic salmon of simple sequence repeats (SSRs) linked to genes of known function (*i.e.* type I genetic markers; Ng *et al.*, 2005) is also opening the possibility for detecting adaptive variation and signatures of divergent selection in this species using microsatellite markers (e.g. Rynänen & Primmer, 2004; Vasemägi, Nilsson & Primmer, 2005). The combined use of neutral and non-neutral markers (e.g. Consuegra *et al.*, 2005*c*; Langefors, 2005) targeting different functional and biological levels (reviewed in Vasemägi & Primmer, 2005) should help to clarify the relative importance of adaptive evolution in relation to gene flow, mutation and drift.

### (3) Agents of selection

Despite ample evidence that natural selection can play a major diversifying role in salmonid populations, identifying specific agents of selection has proved difficult. Studies

in Atlantic salmon and other salmonids indicate that water temperature, stream size (or their correlates), female choice, and predation risk appear to be particularly influential and widespread (Table 6). However, the existence of trade-offs and contrasting selective pressures means that there are probably multiple fitness optima and several adaptive peaks. For example, large male body size at maturity may be selected by female choice, fast currents, and extensive migration distances, and be selected against by bear predation, low flows, and risk of stranding (Table 6). The strength and direction of different selective pressures, hence, can differ substantially between salmon populations (e.g. Quinn & Kinnison, 1999).

### III. LOCAL ADAPTATIONS, CONSERVATION AND MANAGEMENT: BEYOND PASCAL'S WAGER

There is, we have seen, a substantial body of circumstantial evidence that suggests that populations of Atlantic salmon - like those of many other salmonids - show inherited adaptive variation (Quinn & Dittman, 1990; Taylor, 1991; Quinn *et al.*, 1998, 2000; Quinn, Hendry & Buck, 2001*a*; Altukhov, Salmenkova & Omelchenko, 2000; Hendry, 2001; Quinn, 2005). There are also some experimental results and certain patterns of inherited resistance to parasites and diseases that can best be viewed as adaptations to the local environmental conditions. However, the evidence for local adaptations is in all cases incomplete, and their existence continues to be challenged (Adkison, 1995; Bentsen, 1994, 2000; Purdom 2001).

Conditions that may promote the development of local adaptations on theoretical grounds (Taylor, 1991; Adkison, 1995) are summarised in Table 7 and show that the emergence of locally adapted populations, and the extent and strength of adaptive variation, probably follows a continuum. In general, local adaptations may be expected to be favoured amongst large populations that exchange few migrants, and are subjected to strong selective pressures in relatively predictable habitats (Kawecki & Ebert, 2004). However, the existence of interactions between habitat quality, population size and asymmetric dispersal within metapopulations (Consuegra *et al.*, 2005*d*; Consuegra & Garcia de Leaniz, 2006), means that the scale and extent of local adaptations may be highly variable and not easily inferred from simple measures of gene flow (Taylor, 1991; Hansen *et al.*, 2002). For example, populations inhabiting peripheral or marginal habitats may be exposed to stronger selective pressures (conducive of local adaptations) than those at the centre of the distribution, but also to increased dispersal (conducive of gene flow) and greater fluctuations in population size that may constrain adaptive differentiation. Similarly, the scope for local adaptations in peripheral populations may depend critically on whether they are located at the 'leading' (founder) or 'rear' (ancestral) edges of the species range (Hampe & Petit, 2005).

Analysis of comparative life-history data (Figs 4–5) indicates that anadromous Atlantic salmon populations

Table 6. Presumed agents of selection and inferred adaptive phenotypic response (+ increase, – decrease) in several studies of salmonids. Species: AS: Atlantic salmon (*Salmo salar*), BT: brown trout (*S. trutta*); SS: Sockeye salmon (*Oncorhynchus nerka*); CK: Chinook salmon (*O. tshawytscha*); CM: chum salmon (*O. keta*); CO: coho salmon (*O. kisutch*); PS: pink salmon (*O. gorbuscha*), RT: rainbow trout (*O. mykiss*); CT: cutthroat trout (*O. clarkii*)

Presumed agent of selection	Dependent phenotypic trait	Inferred adaptive response	Species	Reference
Water temperature	Alevin size	+/-	CM	Beacham & Murray (1985)
Water temperature	Breeding time	+	AS	Fleming (1996)
		+	AS	Heggberget (1988)
		+	PS	Sheridan (1962)
		+	CK	Burger <i>et al.</i> (1985)
		+	CK, SS	Quinn (2005)
		+	SS	Brannon (1987)
Water temperature	Timing of river entry	+/-	AS	Solomon & Sambrook (2004)
Summer flow	Juvenile size	+/-	AS	Good <i>et al.</i> (2001)
Low dissolved oxygen	Egg size	+	AS, BT	Einum <i>et al.</i> (2002)
Water velocity	Fin size	+	AS	Claytor <i>et al.</i> (1991)
		+	AS, BT	Pakkasmaa & Piironen (2001 <i>b,a</i> )
Water velocity	Body streamlines	+	AS	Claytor <i>et al.</i> (1991)
		+	BT	Pakkasmaa & Piironen (2001 <i>a</i> )
Water velocity	Body depth	+	AS	Pakkasmaa & Piironen (2001 <i>b</i> )
Gravel size	Egg size	+	SS	Quinn <i>et al.</i> (1995)
		+	SS	Quinn (2005)
Stream size	Age at maturity	+	SS	Quinn (2005)
Migration distance	Female length	–	CK	see Quinn (2005)
Migration distance	Swimming stamina	+	CO, RT	see Taylor (1991)
Migration distance	Egg size	–	CK, SS, CM	see Einum <i>et al.</i> (2004)
		–		Healey (2001)
Migration distance	Ovary mass	–	CK, SS, CM	see Einum <i>et al.</i> (2004)
Migration distance	Iteroparity	–	AS	Jonsson <i>et al.</i> (1997)
Inlet/outlet location	Rheotactic response	+/-	RT	see Taylor (1991)
		+/-	SS	Hensleigh & Hendry (1998)
		+/-	SS, CT, BT	see Quinn (2005)
Inlet/outlet location	Compass orientation	+/-	SS	Quinn (1985)
Competition	Timing of emergence	–	AS	Brännäs (1995)
		–	AS	Garcia de Leaniz <i>et al.</i> (2000)
		–	AS	Einum & Fleming (2000 <i>b</i> )
Competition/predation	Egg size	+	CO	Fleming & Gross (1990)
Competition/predation	Fecundity	–	CO	Fleming & Gross (1990)
Predation risk	Timing of emergence	+	AS	Brännäs (1995)
Predation risk	Cryptic colouration	+	AS	Donnelly & Whoriskey (1993)
Bear predation	Adult size	–	SS	Quinn & Kinnison (1999)
		+	SS	Ruggerone <i>et al.</i> (2000)
		–	SS	Quinn & Buck (2001)
Bear predation	Sex ratio (M/F)	–	SS	Quinn & Buck (2001)
Bear predation	Breeding time	+/-	PS, SS	Gende <i>et al.</i> (2004)
Bear predation	Male body depth	–	SS	Quinn & Kinnison (1999)
		–	SS	Quinn & Buck (2001)
Sawbill duck predation	Smolt size	+	AS	Feltham & MacLean (1996)
		+	AS	Feltham (1990)
Risk of stranding	Adult size	–	SS	Quinn & Buck (2001)
Female choice	Male adipose fin	+	AS	Järvi (1990)
		+	BT	Petersson <i>et al.</i> (1999)
Female choice	Male kype/hooks nose	+	CO	Fleming & Gross (1994)
Female choice	Male breeding colouration	+	SS	Craig & Foote (2001)
Female choice	Male body size	+	SS	Quinn & Foote (1994)
Female choice	Male dorsal hump	+	SS	Quinn & Foote (1994)
Fishing pressure	Egg size	–	Various	Rochet <i>et al.</i> (2000)
Fishing pressure	Fecundity	+	Various	Rochet <i>et al.</i> (2000)
Fishing pressure	Run timing	+	AS	Consuegra <i>et al.</i> (2005 <i>a</i> )
Fishing pressure	Body size	–	AS	Consuegra <i>et al.</i> (2005 <i>a</i> )
		–	PS	Ricker (1981)
Fishing pressure	Age at sexual maturity	–	AS	Consuegra <i>et al.</i> (2005 <i>a</i> )
		–	PS	Ricker (1981)

Table 7. Conditions that may be expected to favour the development of local adaptations in Atlantic salmon

Condition	Scope for local adaptations	
	Lowest	Highest
1. Geographical distribution	Central	Peripheral
2. Life history	Anadromy	Residency
3. Population growth	Slow	Fast
4. Environment	Unstable	Stable
5. Population size	Small	Large
6. Phylogeny	Recent	Old
7. Selection	Slack	Intense
8. Inter-specific competition	Low	High
9. Genetic variation	Low	High
10. Longevity/life span	Low	High
11. Reproductive strategy	Iteroparity	Semelparity
12. Environment	Uniform	Patchy
13. Reproductive isolation	Low	High
14. Gene flow	High	Low
15. Generation time	Slow	Fast
16. Predation risk	Low	High
17. Food supply	Scarce	Abundant
18. Pathogen/parasite diversity	Low	High
19. Size of watershed	Small	Large
20. Behaviour	Straying	Homing

tend to vary more in fresh water than in the marine environment (Fig. 4). Moreover, phenotypic traits tend to differ more between populations than they differ from year to year within populations, with freshwater traits varying the most among populations and marine traits varying the least, when corrected by the degree of temporal stability (Fig. 5). Population stability and demographic resilience are good indicators of population viability, and thus of extinction risks, for wild salmon populations (Dodson *et al.*, 1998; Einum *et al.*, 2003), while the level of biocomplexity (Michener *et al.*, 2001) resulting from the interaction of discrete spawning populations with local characteristics (Ford, 2004; Consuegra & Garcia de Leaniz, 2006) can buffer against environmental or anthropogenic change (e.g. Hilborn *et al.*, 2003). Thus, conditions conducive to local adaptations seem more likely to occur in fresh water than in the sea, as predicted on theoretical grounds and suggested by earlier work (see Taylor 1991). But, what are the implications for conservation and management, or in other words, how should we be wagering?

In his *Pensées*, Blaise Pascal (1623–1662) put forward three arguments for believing in the existence of God, perhaps the most popular of which is the so-called ‘Pascal’s Wager’: wagering for God can be shown to be distinctly better than wagering against God (Hájek, 2001) because there is little cost in believing in God if He does not exist but there are dire consequences of denying God if He indeed does exist. This is, of course, essentially the same argument embedded in risk management and the precautionary approach applied to fisheries (Dodson *et al.*, 1998; Hilborn *et al.*, 2001). In the case of Atlantic salmon, the implications of

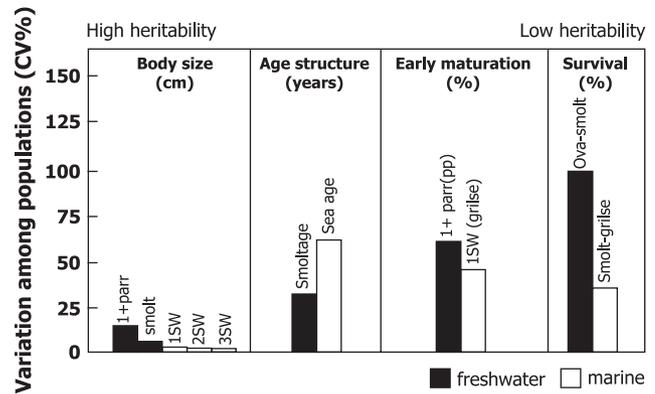


Fig. 4. Variability in several fitness-related traits for Atlantic salmon populations, expressed as coefficient of variation (CV, %) around the interpopulation mean, calculated from data in Hutchings & Jones (1998). Original data has been log-transformed (body size, age) or arcsine-transformed (proportions) before calculating a corrected coefficient of variation (Sokal & Rohlf, 1995). Anadromous populations tend to vary more in fresh water than in the marine environment. SW, seawinter.

ignoring the existence of locally adapted populations when they do in fact exist are much worse than the risk of managing for local adaptations when there are none (Table 8).

Since the phenotype is the result of the interaction between the genotype and the environment, it follows that changes in either the genes or the habitat have both the potential for altering the degree of adaptation and fitness of Atlantic salmon populations. Four general problems leading to the loss of adaptive variation can be envisaged, depending on whether the alteration is in the genes or the environment (see also Dodson *et al.*, 1998).

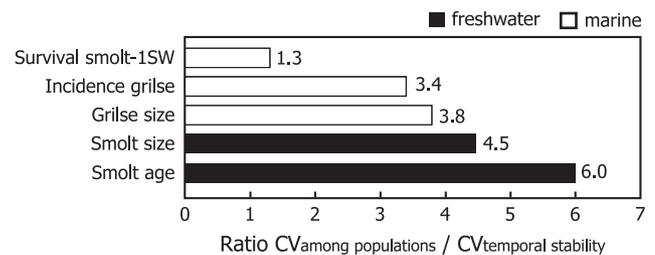


Fig. 5. Ratio between the variability observed in several phenotypic traits among populations, expressed as the coefficient of variation (CV) around transformed population means, and the temporal stability within populations (expressed as the arithmetic mean of the annual coefficients of variation) calculated from data in Hutchings & Jones (1998) and incorporating the correction for CV from Sokal & Rohlf (1995). The results indicate that in all cases phenotypic traits differ more between populations than they differ from year to year within populations (i.e. ratio > 1.0). Freshwater traits vary the most among populations while marine traits vary the least, when corrected by the degree of temporal stability.

Table 8. Pay-off matrix for considering local adaptations (LA) in Atlantic salmon management

	LA exist	LA do not exist
Wager for local adaptations	Gain all: - proper, proactive management	<i>Status quo:</i> - unnecessary expenditure
Wager against local adaptations	Lose all: - risk of serious mismanagement - erosion of adaptive variation - increased risk of extinction	<i>Status quo:</i> - saving of management resources

### (1) Loss of fitness due to genetic changes

In line with Fisher's (1958) tenet of two opposing forces of evolution, the fitness of an organism is augmented in each generation by natural selection and eroded by mutation and environmental change. Thus, at least in constant environments, genetic variation can have both benefits (improves future adaptive potential) but also costs (reduces current adaptation). Genetic changes leading to loss of adaptive potential may result from deleterious mutations, gene introgression or random genetic drift. Two possible scenarios can be visualised, one in which the genotype (and thus probably the phenotype) shifts from an adaptive peak, and one in which the population simply becomes more vulnerable to environmental change.

#### (a) Problem #1. Genotype/phenotype shifts from adaptive peaks

The deliberate (e.g. stocking) or accidental (e.g. farm escapes) introduction of non-native salmon may result in the introgression of poorly adapted genes into local salmon populations, and this may lead to outbreeding depression and maladaptation (Waples, 1994; Gharrett *et al.*, 1999; Utter, 2001; Hallerman, 2003). Native Atlantic salmon populations generally survive and perform better than non-native populations (Garcia de Leaniz, Verspoor & Hawkins, 1989; Verspoor & Garcia de Leaniz, 1997; Donaghy & Verspoor, 1997; McGinnity *et al.*, 2003). This means that accidental escapes of farm salmon (or deliberate introductions *via* stocking of non-native salmon) may be expected to reduce the survival and productivity of wild native populations should they interbreed. Repeated introductions will produce cumulative fitness depressions and could potentially result in an extinction vortex in vulnerable populations (McGinnity *et al.*, 2003).

However, the impact of foreign introductions may also depend on the density of native fish in the river. Thus, where the river is below carrying capacity, the introduced fish may survive alongside the native individuals, and this may initially result in an overall increase in the production of smolts and adults. Hybridisation between native and non-native individuals may conceivably increase the overall fitness of the wild population in the first generation (e.g. Einum & Fleming, 1997), though hybrid vigour appears to be rare in salmonids (McGinnity *et al.*, 2003) or, indeed, in other freshwater fishes (e.g. Cooke, Kassler & Philipp, 2001). Depending on the extent of hybridisation, fitness is likely to be reduced in subsequent generations, possibly to

a value below that prior to the introduction (e.g. as seen in song sparrows *Melospiza melodia*: Marr, Keller & Arcese, 2002). On the other hand, where a river is already at carrying capacity, introductions can reduce wild smolt production and reduce fitness in the first generation (Einum & Fleming, 2001). Deliberate introductions of farmed salmon in such situations are particularly damaging due to behavioural displacement of wild fish by farm parr, with subsequent poor marine survival of farm fish resulting in an overall reduction in adult returns (e.g. McGinnity *et al.*, 2003). Farm escapes entering a river generally result in hybrids rather than in pure farm offspring due to differential spawning behaviour of males and females (Fleming *et al.*, 2000). Again, such hybrids may displace wild fish and lower the population's overall fitness. The lower fitness of non-native wild fish means that deliberate introductions of such fish are just as damaging as farm escapes. Indeed, such introductions may be more damaging since relatively greater numbers may be involved with annual introductions rather than periodical ones as typical of farm escapes.

Theodorou & Couvet (2004) have recently shown that, at least for some species, supplementation programs could help in the recovery of endangered populations, provided family sizes are equalized, the size of the captive population is reasonably large ( $N > 20$ ), and introductions are carried out at a low level (1–2 individuals/generation) and over a limited time period (<20 generations). Unfortunately, few of these conditions can be met in salmonid stocking programmes, where family sizes can rarely be equalized, and a trade-off exists between maximizing offspring survival in the hatchery and maintaining genetic diversity (Fiumera *et al.*, 2004).

Salmonid hatcheries usually release tens, or even hundreds of thousands, of individuals and their role in fisheries management remains highly controversial (Meffe, 1992; Myers *et al.*, 2004; Brannon *et al.*, 2004). For example, domestication (the adaptation of individuals to the artificial environment) may shift allelic frequencies, or even result in the fixation of deleterious alleles that cannot be purged after stocking ceases (Lynch & O'Hely, 2001), and the introduction of maladapted individuals could potentially reduce the fitness of natural populations (Tufto, 2001; Ford, 2002), thus negating the apparent, short-term benefit of increased abundance. The release of hatchery-reared salmonids can in some cases hinder, rather than aid, the recovery of endangered populations (e.g. Levin *et al.*, 2001; Levin & Williams, 2002), and there is increasing concern about the

genetic risks associated with large-scale stocking practices and the consequences of intra-specific hybridization (e.g. Vasemägi *et al.*, 2005). Homing ability in salmonids is heritable (reviewed by Stabell, 1984; Quinn, 1993; Hendry *et al.*, 2004a) and hatchery-reared fish (Jonsson, Jonsson & Hansen, 2003) and hybrids (Candy & Beacham, 2000) tend to stray significantly more than pure, wild fish (but see Gilk *et al.*, 2004). Hence, hybridization between wild and hatchery-reared fish (even if these are of native origin) may result in increased gene flow and genetic homogenization, which could cause a breakdown of local adaptations and loss of fitness.

The exploitation of salmon can also erode adaptive genetic variation and negate the fitness benefits of local adaptations, especially when harvesting takes place only at particular times, or concentrates on fish with particular traits (Hard, 2004). For example, Consuegra *et al.* (2005a) have shown that in Iberian salmon populations, anglers selectively exploit early running fish, which differ phenotypically (sea age, smolt age, body size) and genetically (*MEP-2\**, mtDNA) from late-running fish, which tend to escape the fishery. Thus, fishing closures originally designed to protect stocks from overfishing may inadvertently cause a differential mortality of stock components that is likely to be detrimental. In general, selective harvesting in relation to fitness traits may be expected to cause changes in reaction norms (Hutchings, 2004; Hard, 2004) leading to a reduction in fitness in exploited fish populations (Law, 2000, 2001; Conover & Munch, 2002). In addition to run timing, other examples of selective harvesting in salmon include the over-exploitation by anglers of fish in particular pools, or the harvesting of the largest individuals in the drift net fisheries.

(b) *Problem #2. Impoverished gene pool*

Just as foreign introductions and selective harvesting can erode adaptive variation by causing the genotype to shift away from an adaptive peak, an impoverished gene pool can also cause populations to become more vulnerable to environmental change, curtailing their capacity to adapt and increasing the risk of extinction (reviewed by Wang, Hard & Utter, 2002a). Although studies on the effects of inbreeding depression in salmonids are few (reviewed by Wang, Hard & Utter, 2002b), they tend to reinforce the importance of maintaining genetic variation within populations as a primary goal of conservation and management. Maintenance of genetic diversity will be particularly important for fitness in heterogeneous and fluctuating environments with many adaptive peaks because the benefits of maximizing future adaptive potential will generally outweigh the fitness loss of deviating from an 'optimal' genotype (Bürger & Krall, 2004).

Small inbred populations and those subjected to recurring bottlenecks are particularly at risk of losing genetic variation due to random loss or fixation of alleles. The populations of North American desert fish (*Poeciliopsis monacha*) studied by Vrijenhoek (1994, 1996) provide perhaps one of the best examples of how a reduction in genetic diversity (caused by decline in population size) can

cause a reduction in fitness, as evidenced by an increase in the incidence of deformities and greater susceptibility to parasites. In such situations, the influence of genetic drift outweighs the effects of natural selection, further restricting the capacity of the populations to adapt (Lande, 1988; Hedrick, Parker & Lee, 2001). This may be particularly true for small populations of salmonids, because these show a higher temporal variation in population size than larger ones (Einum *et al.*, 2003). Evolutionary theory predicts that in small populations the main diversifying force is genetic drift (Lande, 1988) and that local adaptations are favoured in large and stable populations (Adkison, 1995; but see Ardren & Kapuscinski, 2003). Thus, for natural selection to operate at maximum efficiency, salmon populations need to be large enough and be maintained above a certain size, though determining such minimum viable population size is not an easy task (Ford, 2004; Young, 2004) since small salmon populations can still maintain relatively high levels of genetic diversity despite evidence of recurrent bottlenecks (e.g. Consuegra *et al.*, 2005d).

(2) **Loss of fitness due to changes in the environment**

Environmental change and subsequent phenotypic adjustment may be the norm, but there is growing concern that humans may be altering freshwater ecosystems beyond the capacity of many aquatic organisms to adapt (Carpenter *et al.*, 1992). Fitness may decrease if environmental change is either too great (Problem #3) or too rapid (Problem #4, see below).

(a) *Problem #3. The environment changes too much*

Human-induced environmental change is possibly the most important factor causing species declines worldwide (Sih, Jonsson & Luikart, 2000), including the Atlantic salmon (WWF, 2001). Yet, understanding of how species respond to anthropogenic change and fragmentation at the population level is unclear, though the level of biocomplexity (Hilborn *et al.*, 2003) and the magnitude of perturbations in relation to natural boundaries of environmental variation (Mangel *et al.*, 1996) seem important. Natural selection may be expected to result in individuals most capable of surviving under the historical environmental conditions experienced by each population, within the constraints imposed by the amount of genetic variation and the genetic architecture of adaptive traits. Compared to other sympatric freshwater species, Atlantic salmon tend to show relatively narrow habitat breadths and more stringent habitat requirements (Gibson, 1993; Heggenes, Baglinière & Cunjak, 1999; Klemetsen *et al.*, 2003; Tales, Keith & Oberdorff, 2004), which is one reason why the species is generally regarded as a good indicator of stream quality and biotic integrity (Hendry & Cragg-Hine, 2003; Cowx & Fraser, 2003). For example, adult salmon spawn within a narrower range of stream gradients and particle sizes, and the embryos have far greater requirements for dissolved oxygen and low suspended solids, than most other non-salmonid species (Mann, 1996; Armstrong *et al.*, 2003).

Although there is a general paucity of information on population variation in habitat preferences among salmonids (but see Bult *et al.*, 1999), it seems natural to assume that the habitat preferences of each population are those under which each population performs best. Thus, loss of fitness and eventual extinction may occur if the environment changes beyond the species' habitat requirements or the population preferred optimum. For example, given the observed association between timing of return, age at maturity, and spawning within the river catchment (Webb & McLay, 1996; Stewart *et al.*, 2002; Dickerson *et al.*, 2005) habitat fragmentation and barriers that impede, or simply delay, upstream migration are likely to have negative effects on fitness since run timing in salmonids appears to be a population-specific trait of potential adaptive value (Quinn, 2005; Hodgson *et al.*, 2006).

In general, those habitat changes that may be expected to be most damaging are those that affect reproduction and the critical times for survival, depending on the relative roles of density-dependent and density-independent factors on the survival of each population (Jonsson, Jonsson & Hansen, 1998; Armstrong *et al.*, 2003). Thus, for most salmonids, whose critical time for survival occurs during the early alevin stages and dispersal from the redd (Elliott, 1994), loss of spawning grounds and changes in the quality of nursery areas are likely to be particularly detrimental when competition for resources is intense and survival is density-dependent.

(b) *Problem #4. The environment changes too rapidly*

Maladaptation and loss of fitness may also occur if the environment changes faster than the population can adjust (but see rapid evolution below). This is true even if the magnitude of the environmental change is relatively small, well within the tolerance limits for the population. Examples of rapid environmental changes may include many anthropocentric disturbances such as deforestation, stream regulation, siltation, point-source pollution or blockage of migratory routes (see Mills, 1989; Meehan, 1991; WWF, 2001). These may constitute for salmonids 'ecological traps', i.e. sudden alterations of the environment that can result in inappropriate behavioural or life-history responses based on formerly reliable environmental cues (Kokko & Sutherland, 2001; Schlaepfer, Runge & Sherman, 2002). For example, the discharge cycle of some hydro-power stations may cause adult salmonids to strand or to ascend the rivers at inappropriate times of the year (Mills, 1989).

Other, less rapid sources of environmental change may include climate change. Global climatic change has the potential to alter the adaptive genetic response of aquatic organisms (Carpenter *et al.*, 1992), including that of salmonids (Minns *et al.*, 1992; Magnuson & DeStasio, 1997; McCarthy & Houlihan, 1997). Climatic records indicate that average global temperatures have increased over recent decades in a highly anomalous trend (Jones *et al.*, 1998; Mann, Bradley & Hughes, 1999) resulting in correlated seasonal weather patterns in both the freshwater (Ottersen *et al.*, 2001; Bradley & Ormerod, 2001) and

marine environments (Dickson, 1997; Rahmstorf, 1997). In the case of fresh water, most available evidence indicates a warming trend (Webb, 1996). For example, in the Girnock Burn, a tributary of the Aberdeenshire Dee in Scotland, average annual temperatures in the spring period, which are critical for seasonal growth (Letcher & Gries, 2003) and for smolt migration, have increased by about 2°C since the mid-1960s. These changes were attributed to reduced trends for snowpack accumulation and ablation (Langan *et al.*, 2001). In the River Asón (northern Spain), a similar 2°C increase in water temperature was observed since 1950, coinciding with a decline in abundance and a change in genetic structure of the native Atlantic salmon population (Consuegra *et al.*, 2002). Radio-tracking studies have shown that adult salmon may delay, or even fail, to ascend rivers during hot dry summers (Solomon & Sambrook, 2004), and suggest that recent climate change may be particularly damaging for the survival of southern stocks (Beaugrand & Reid, 2003).

Significant climatic warming has also occurred in the surface waters of the eastern North Atlantic (Dickson & Turrell, 1999), and recent studies provide strong evidence that this is having a major effect on the distribution and abundance of marine fish (Genner *et al.*, 2004; Perry *et al.*, 2005). Given evidence for declining trends in salmon survival at sea (Reddin *et al.*, 1999; Youngson, MacLean & Fryer, 2002), there is growing evidence that recent climatic effects are also unfavourable for Atlantic salmon (reviewed by Friedland, 1998; Beaugrand & Reid, 2003). Considering the thermal niche of Atlantic salmon (Jonsson *et al.*, 2001), and given the dominant influence of water temperature on salmonid growth and life history (Magnuson & DeStasio, 1997; McCarthy & Houlihan, 1997), it is likely that a trend towards warmer temperatures in the east and cooler temperatures in the west would be accompanied by a change in selective pressures and in adaptive genetic variation (e.g. Verspoor & Jordan, 1989). Certainly, Atlantic salmon catches seem to have varied markedly in the historical past (Summers, 1993; Lajus *et al.*, 2001; Youngson *et al.*, 2002), although catch statistics alone should always be used with caution to infer historical changes in salmon abundance (Crozier & Kennedy, 2001). Over recent decades, marine mortality appears to have affected population components differentially (Youngson *et al.*, 2002) and selection may therefore have been involved. In the case of sockeye salmon, climatic variation appears to be linked with major fluctuations in abundance (Finney *et al.*, 2002) and timing of return to fresh water (Hodgson *et al.*, 2006), suggesting that increased and relaxed selection may alternate over long periods. Hilborn *et al.* (2003) have shown that under these conditions the level of biocomplexity in life-history traits of neighbouring salmon stocks is critical for maintaining their resilience to environmental change.

### (3) Rapid evolution

Environmental change, whether natural or anthropogenic, will tend to erode fitness (Fisher, 1958), but just how rapidly and to what extent can salmon populations adjust? Studies

of ‘rapid’ or contemporary evolution (Stockwell, Hendry & Kinnison, 2003) provide insight into this question by showing the ability of populations to undergo adaptive evolution and to adapt to environmental change.

Large phenotypic changes have taken place after 2,000 years of domestication in carp (*Cyprinus carpio*) (Balon, 2004), but recent studies are also uncovering fast rates of evolution in natural fish populations. Empirical evidence for rapid evolution in fish comes mostly from studies on Trinidadian guppies (Reznick *et al.*, 2004), introductions of Pacific salmonids into New Zealand (Kinnison & Hendry, 2001, 2004), and translocations of European grayling (*Thymallus thymallus*) between Scandinavian lakes (Koskinen *et al.*, 2002). Results for salmonids (Table 9) indicate that adaptive divergence in life history traits can take place in as few as 8 generations, even within small bottlenecked populations. Translocations of sockeye (Hendry *et al.*, 2000; Hendry, 2001) and chinook salmon (Kinnison *et al.* 2001; Quinn, Kinnison & Unwin, 2001*b*; Unwin *et al.*, 2000, 2003) have also resulted in significant and mostly predictable changes in morphology, reproductive investment, growth and timing of return that testify to the strength of divergent selection.

However, how can anadromous salmon populations be locally adapted and yet perform well (and evolve rapidly) outside their native range? It seems that for salmonids, one consequence of living in highly changing aquatic environments may have been the development of considerable phenotypic plasticity, which may itself have been the target of selection (Jørstad & Nævdal, 1996; Pakkasmaa & Piironen, 2001*a*). Thus, the same phenotypic plasticity that may have allowed salmonids to adapt to local environmental conditions may also have allowed them to perform successfully in a variety of aquatic habitats (Klemetsen *et al.*, 2003) and to evolve rapidly outside their native range (Taylor, 1991; Kinnison & Hendry, 2004).

Ultimately, knowledge of adaptive genetic variation is needed to understand why hatchery-reared fish are failing to survive in the wild, why escapes from fish farms pose a threat to natural populations, or how exploitation and environmental change are impacting upon wild stocks.

#### IV. CONCLUSIONS

(1) In the Atlantic salmon, one of the most extensively studied fish species, and a model system in conservation and evolutionary biology, the case for local adaptation is compelling but the evidence relating to its exact nature and extent remains limited.

(2) The scale of adaptive variation most probably varies along a continuum, depending on habitat heterogeneity, environmental stability, and the relative roles of selection and drift. Analysis of life-history data in Atlantic salmon indicates that phenotypes differ more between populations than they differ from year to year within populations, with freshwater traits varying the most and marine traits varying the least when corrected by the degree of temporal stability. Conditions conducive to local adaptations, hence, appear to be more likely to occur in freshwater than in the sea. Water temperature, photoperiod, and stream morphology (and correlated variables) appear to be amongst the strongest and most stable physical variables determining local selective pressures across the species’ range. Other important agents of selection for anadromous salmonids include migration distance, mate choice, and predation risk.

(3) Genotype-by-environment interactions are detected for many traits in Atlantic salmon, including body size, growth, age at sexual maturity, timing of alevin emergence, aggressive behaviour, tolerance to low pH, and resistance to various diseases. Such interactions suggest that different genotypes may be optimal under different environments, thereby providing conditions for local adaptations to develop.

(4) Information on the adaptive significance of molecular variation in Atlantic salmon and other salmonids remains scant and largely circumstantial. Variation at MHC genes arguably provides the best evidence for selection at the molecular level, but much more work is needed to understand the adaptive implications of molecular variation among populations. Analysis of quantitative trait loci, and the application of functional genomic techniques, will likely

Table 9. Studies showing ‘rapid evolution’ in salmonids illustrating the extent and rate of adaptive change in translocated populations over contemporary time scales (reviewed in Kinnison & Hendry, 2001, 2004)

Species	Origin	Translocated to	Diverging traits	Time scale (generations)	Reference
Chinook salmon ( <i>Oncorhynchus tshawytscha</i> )	Various N. America	New Zealand	Ovarian production Morphology Run timing Growth Survival	30	Kinnison <i>et al.</i> (2001) Quinn <i>et al.</i> (2001 <i>b</i> ) Unwin <i>et al.</i> (2000, 2003)
Sockeye salmon ( <i>O. nerka</i> )	Baber Lake (USA)	Lake Washington (USA)	Morphology	13	Hendry <i>et al.</i> (2000) Hendry (2001)
European Grayling ( <i>Thymallus thymallus</i> )	Various Norway	Several Norwegian lakes	Age at maturity Size at maturity Fecundity	8–28	Haugen (2000 <i>a,b</i> ) Koskinen <i>et al.</i> (2002) Haugen & Vollestad (2001)

play a major role in unravelling the true extent of adaptive variation on this species in the future.

(5) Regardless of the true extent of adaptive variation, the implications of ignoring the existence of locally adapted populations when they exist are much worse than the risk of managing for local adaptations when there are none. Four general problems can lead to loss of fitness and mismanagement if local adaptations are ignored:

(a) *genotype shifts*, when the genotype, and likely the phenotype, shift outside an adaptive peak, for example due to outbreeding depression (e.g. resulting from the deliberate or accidental introduction of maladapted individuals) or from the selective exploitation of particular phenotypes (e.g. fish of larger size).

(b) *loss of genetic diversity* following population bottlenecks (for example due to overexploitation or introduction of non-native diseases), which may result in inbreeding depression causing salmon populations to become more vulnerable to environmental change, curtailing their capacity to adapt, and increasing the risk of extinction.

(c) *loss of habitat quality* leading to phenotypic mismatch, if the environment is pushed beyond the species' habitat requirements, or more typically, beyond the population's adaptive zone, and

(d) *rapid environmental change* resulting in maladaptation, if changes in the environment are simply too rapid, making it impossible for local phenotypes to adjust.

(6) Despite extensive screening of phenotypic and genetic variation in Atlantic salmon and other salmonids over the last two decades, limited progress has been made in uncovering the nature and extent of adaptations. Some areas where work might be fruitful include the following:

(a) *Extent of local adaptations*. Ecological correlates and breeding studies have shed some light on the genetic basis of adaptive trait divergence, but only common-garden field experiments and reciprocal transfers are capable of disentangling the effects of phenotypic plasticity from additive genetic effects, and to uncover or rule out the existence of local adaptations. Unfortunately, few such studies exist and their importance cannot be overemphasized, since legal protection of endangered stocks (including protection from the expansion of salmon farming) rests largely upon the tenet that wild populations are locally adapted and that introgression with farmed stocks will be detrimental.

(b) *Heritability of fitness-related traits*. Much information is available on trait heritability of cultured stocks but its relevance to natural populations is unclear. Field heritability estimates are required for predicting the likely evolutionary response of wild populations to environmental change, fisheries exploitation, or introgression with farmed fish. Do salmon populations differ in additive genetic variance for a given trait? Can we infer the strength of natural selection on different traits from their heritability values?

(c) *Extent of phenotypic plasticity and genotype-by-environment interactions*. Understanding the extent of phenotypic and genotypic resilience in relation to temporal fluctuations in the freshwater and marine environments is essential for understanding the nature of the adaptive response. What is the extent of phenotypic plasticity for life-

history traits in salmon? How is phenotypic plasticity related to environmental predictability and generation length? Are short-lived populations, or those living in more variable environments, more plastic than long-lived ones?

(d) *Agents of selection*. Relatively little is known about specific agents of selection affecting salmonids, or how wild populations respond to multiple and often contrasting selective pressures. What is the strength of artificial selective pressures, such as fish culture, fisheries exploitation or human-induced environmental change compared to natural and sexual selection?

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