# 7 Local Adaptation

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Upper: the River Ason at Marron, in northern Spain, at the southern limit of the Atlantic salmon distribution. Lower: the Kapisidlit River in West Greenland, less than 10 km from the main ice sheet, Greenland's only river with a self-sustaining run of salmon. (Photos credit: E. Verspoor.)
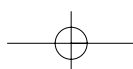
The tendency of salmon, *Salmo salar*, to return from the sea to the river of hatching and form 'local populations' has apparently been known for a long time (Calderwood 1908). Writing in 1653, Izaak Walton described how juveniles marked with ribbons tied to their tails were later recaptured as adults in their home river. Since no two rivers are completely identical, salmon returning to spawn in different rivers will, with time, give rise to different strains or 'races' (Huntsman 1941). Those races, so the story goes, are presumably the ones best 'adapted' to the local river conditions. But, is this really the case? And if so, what are local salmon adapted to? And perhaps more importantly, why should we care about it?

In this chapter we will examine the evidence for (and against) the existence of local adaptations in Atlantic salmon, in particular those studies that have become available during the last decade, since Taylor (1991) reviewed this subject. We will also consider the implications of adaptive variation for the management and conservation of Atlantic salmon populations. But first we must define what we mean by 'adaptation'.

7.1 Introduction

Ever since Darwin (1859) first introduced the concept of 'adaptation', there has not been an entirely satisfactory definition of what adaptation really means (Reeve and Sherman 1993; De Jong 1994; Rose and Lauder 1996), which is perhaps surprising considering its central role in evolutionary theory and in the philosophy of biology (Hull 1974). Darwin described an adaptation as any feature of an organism that arose as a consequence of natural selection and hence enhances the fitness of the individual. He recognised that:

- one trait might be functionally linked to another, so that the response to selection of one trait could cause changes in others that were not necessarily adaptive;
- various forms of constraints could limit the ability to adapt or change in response to natural selection; and
- the traits of an organism are laden with its history and are not necessarily representative of optimal adaptation to current conditions.

However, Darwin himself was puzzled by how some adaptations came about in such apparently purposeful manner (the complex structure of the human eye being a case in point) and recognised the danger of a circular, tautological argument (Ruse 1982; Reid 1985). Some conceptual difficulties arise when adaptation is sometimes taken to mean a 'process' (birds may be said to have adapted to flying), while at other times it refers to an 'outcome' or 'feature' (feathers constitute an adaptation to flying). Problems are also encountered when, without the benefit of invoking teleological concepts of 'purpose' or 'design', it becomes necessary to determine which traits are adaptive and which traits are not (not everything is adaptive; Gould and Lewontin 1979). Finally, there is no consensus as to whether it is the genotype, the phenotype, the individual or the population that is 'adapted' (see Reeve and Sherman 1993), nor is it clear what are the relative roles of selection, mutation and chance in shaping the way organisms respond to local environmental conditions.

Perhaps the easiest way to view adaptation (the process) is to consider it as 'the good fit of organisms to their environment' (Gould and Lewontin 1979), and to regard adaptation (the outcome) as 'any feature that promotes fitness' (Gould and Vrba 1982; Mayr 2002).

7.1.1 *Phenotypic diversity and fitness in a changing world*

Environments are rarely constant or perfectly predictable, so there is never a single phenotype that can outperform the others under all environmental conditions. Frequency-dependence makes it possible for several phenotypes to coexist in an evolutionary stable state (Maynard Smith 1982) and phenotypic diversity is therefore the norm. Since natural selection can only act on existing designs, most phenotypes are also bound to be maladapted to some extent (see Box 7.1).

In his shifting-balance theory of evolution, Wright (1932) introduced the concept of 'adaptive landscape' to help visualise how the fitness of individuals would change under various conditions of selection intensity, mutation rates and environmental change. In Wright's three-dimensional model, allele frequencies are plotted against fitness and the resulting landscape resembles a topographical map, with adaptive peaks and valleys representing points of high and low fitness (see Hallerman 2003a). Similar, albeit simpler, diagrams showing how fitness may vary with temporal changes in the environment and in the phenotype are shown in Boxes 7.1 and 7.2. Here, fitness can be viewed as the degree of matching between phenotype and environment (Box 7.1, Fig. B7.1), being augmented in each generation by natural selection and eroded by mutations and changes in the environment (Box 7.2, Fig. B7.2).

7.2 Scope for local adaptations in Atlantic salmon

Local adaptations are presumed to exist when the average fitness of local individuals exceeds the average fitness of immigrants (Lenormand 2002). However, deciding where to draw the line between 'local' and 'foreign' individuals (i.e. setting geographical boundaries to populations) constitutes an unresolved problem for most salmonid populations (Riddell 1993; Waples 1995; Morán 2002, but see Chapter 5). Whatever their geographical limits, for local adaptations to develop, three essential conditions must first be met (Allendorf and Waples 1996):

- there must be genetic variation in fitness related traits, both within and among populations;
- populations must be subjected to different selective regimes with different genetic optima; and
- populations must be reproductively isolated to some extent (i.e. the strength of selection must exceed the level of gene flow).

The evidence for each of these in Atlantic salmon will be examined next.

7.2.1 *Genetic variation in fitness-related traits*

The existence of adaptive genetic variation is the first essential requirement for Atlantic salmon populations to evolve and for local adaptations to develop. For a given environment, some genotypes are more successful at surviving and reproducing than others and natural selection acts based on these differences. Relative fitness, the combined ability to survive and reproduce, is the measure of selection at the individual level.

Although the amount of genetic variation in Atlantic salmon for 'neutral' markers was once thought to be somewhat limited when compared to other salmonids (Altukhov *et al*. 2000),

this is no longer considered to be the case. Significant genetic differences are found between major groupings separated thousands of kilometres but also among populations inhabiting nearby tributaries of major river systems (e.g. Fontaine *et al*. 1997; Spidle *et al*. 2001; Verspoor *et al*. 2002, 2005; Chapter 5). Genetic variation in Atlantic salmon is distributed hierarchically among three major geographical areas (Western Atlantic, Eastern Atlantic and Baltic), among different lineages within each area (e.g. northern and southern lineages within the Baltic), among river systems and among tributaries within river systems (Chapters 5 and 6). Although not available specifically for Atlantic salmon, most estimates of mutation rates suggest that they play a negligible role in generating differences among populations on the postglacial time scale relevant for Atlantic salmon populations (Hartl and Clark 2000). Therefore, many studies have attempted to estimate only the relative strengths of genetic drift and gene flow by using molecular markers that are usually assumed to be selectively neutral, but in general results are consistent among studies and reveal limited levels of gene flow (Verspoor *et al*. 2005; Chapter 5).

While knowledge of levels and patterns of neutral genetic variation in Atlantic salmon is well developed (Chapters 5 and 6), there is relatively little comparable information on heritable variation in quantitative traits (acquired principally through rearing individuals from differ-ent populations in a common environment). Under most (but not all) conditions, heritable variation in quantitative traits may be expected to mimic genetic variation in 'neutral' markers (Reed and Frankham 2001; Hendry 2002). However, it appears that populations may be more differentiated at loci coding for quantitative traits than at neutral loci (Lynch *et al*. 1999; Merilä and Crnocrak 2001; McKay and Latta 2002). Estimates of population differentiation from molecular markers (which are available for Atlantic salmon) may, therefore, underest-imate differentiation at quantitative trait loci (Latta and McKay 2002; Morán 2002), which are believed to be the major targets of selection. There is thus considerable scope for local adaptations to develop even in the absence of strong differentiation at neutral markers: it may only take a difference in one quantitative trait (controlled by a very small part of the genome).

A number of comparisons of populations and families of Atlantic salmon have identified genetic differences in several fitness-related traits, such as survival or energy content/acquisition, in both freshwater and marine stages (Table 7.1). Many of these studies also indicate the existence of genotype-by-environment (G × E) interactions. For example, Jonsson *et al*. (2001) studied five Norwegian salmon 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 that the populations originated from. However, maximum growth efficiencies were greatest in those populations with the lowest opportunities for feeding and growth, suggesting a possible adaptive advantage. G × E interactions in adult body size and survival have also been identified in studies where different populations have been released in different wild locations (e.g. Jonasson 1996; Jonasson *et al*. 1997). In these studies, the popula-tions with the fastest growth and highest survival differed between locations, suggesting that different individual characteristics are required to maximise growth and survival in different environments. A similar conclusion was also indicated in a study of wild female Atlantic salmon; when controlling for differences in smolt age and size, individuals growing the fastest in fresh water grew more slowly at sea (Einum *et al*. 2002; see also Huntingford and García de Leániz 1997 for a discussion of this interaction hypothesis and Niva and Jokela 2000 for similar interactions in brown trout).

Table 7.1 Evidence for genetic variation in fitness related traits among and within populations of Atlantic salmon. Asterisks indicate studies suggesting G × E interactions.

Dependent trait	Reference
Among populations	
Body size	Jonasson (1993), Jonasson *et al*. (1997)*
Digestive rate	Nicieza *et al*. (1994b)
Growth efficiency	Jonsson *et al*. (2001)*
Growth rate	Gunnes & Gjedrem (1978)*, Holm & Fernö (1986), Torrissen *et al*. (1993), Nicieza *et al*. (1994a), Friedland *et al*. (1996), Jonsson *et al*. (2001)*
Survival	Gjedrem & Aulstad (1974), Hansen & Jonsson (1990), Jonasson (1993), Friedland *et al*. (1996), Jonasson (1996), Donaghy & Verspoor (1997), Jonasson *et al*. (1997), Rosseland *et al*. (2001)
Within populations	
Body size	Gjedrem (1979), Friars *et al*. (1990), Rye & Refstie (1995)
Feeding rate	Thodesen *et al*. (2001)
Timing of maturity	Gjerde (1984)
Stress	Fevolden *et al*. (1991)
Growth efficiency	Thodesen *et al*. (2001)
Growth rate	Thorpe & Morgan (1978), Gjerde (1986), Friars *et al*. (1990), Rye *et al*. (1990), Torrissen *et al*. (1993), Thodesen *et al*. (2001)
Sea louse infection	Mustafa & MacKinnon (1999)
Survival	Thorpe & Morgan (1978), Schom (1986)*, Standal & Gjerde (1987)*, Rye *et al*. (1990), Bailey *et al*. (1993)*, Fevolden *et al*. (1993), (1994)*, Gjedrem & Gjøen (1995)*, Lund *et al*. (1995)*, Gjøen *et al*. (1997)*, Langefors *et al*. (2001)*

A special category of studies indicating G × E interactions include those showing differences in performance among populations or families under hostile abiotic conditions, or in susceptibility to diseases and parasites. These have identified distinct population and family responses to viral and bacterial infections and low pH levels (Table 7.1).

7.2.2 Environmental variation and differential selective pressures

Environmental conditions experienced by Atlantic salmon can differ considerably across the species range (Table 7.2), which is a necessary prerequisite for the existence of differential selective regimes and the development of local adaptations. There are at least 2321 salmon rivers (excluding those where the species is now extinct) in North America and Europe (WWF 2001) and the number of Atlantic salmon populations has conservatively been estimated at over 2000 (Saunders and Bailey 1980). In Europe, natural populations of Atlantic salmon are found from Iberia in the south (42°N) to Finnmark and arctic Russia (71°N) in the north (MacCrimmon and Gots 1979; Altukhov *et al*. 2000), thus covering over 3200 km. The natural distribution in North America is less extensive (43°N to 59°N or # 1800 km).

Salmon rivers can be grouped into five biogeographic regions according to geographic location, geology, flow regime, and climate (Elliott *et al*. 1998). Within each biogeographic

Table 7.2 Range of environmental conditions, genetic variation, and phenotypic traits that are known to differ between Atlantic salmon populations inhabiting different locations. The list is not intended to be exhaustive.

Environmental variation	Genetic variation	Phenotypic variation
Physical	*Chromosome structure*	*Abundance and survival*
Latitude and longitude	Karyotype	Population size
Photoperiod	Banding patterns	Spatial distribution
Solar radiation	*Allozymes*	Density
Temperature regime	27 polymorphisms	Intraspecific competition
Rainfall	*Mitochondrial DNA*	Juvenile survival*
Discharge	*Microsatellite DNA*	Adult survival*
Stream order and size	*MHC*	Return rate*
Slope	Class I	Disease and parasite resistance*
Habitat type (lake, river, etc.)	Class II	Resistance to low pH*
Ice cover		*Morphology and physiology*
Microhabitat composition		Body size*
Geology		Body composition*
Water chemistry		Growth efficiency*
Water depth		Growth rate*
Water velocity		Digestive rate*
Substrate		Meristics*
Cover and shade		Morphometrics*
Droughts		Fluctuating asymmetry
Biological		Health condition*
Vegetation		Gamete quality*
Productivity		*Life history and behaviour*
Prey		Diet composition
Fish community structure		Habitat choice
Inter-specific competition		Age at smolting*
Predators		Age at maturity*
Parasites		Longevity*
Pathogens		Movements and migrations*
Anthropogenic disturbances		Timing of spawning*
Human pressure		Timing of hatching/emergence*
Land use		Timing of smolting*
Water abstraction		Run timing*
Obstacles and accessible length		Egg size*
Introduction of foreign species		Fecundity*
Exploitation		Iteroparity*
Recreation		Sex ratio
Pollution and water quality		Reproductive effort
		Male parr maturation*

* Phenotypic traits with a known (or suspected) genetic component.

region the freshwater environment varies somewhat predictably with latitude and altitude (Gibson 1993). Extreme cases refer, for example, to the Ungava Bay area of northern Quebec (Power 1981) or to some Norwegian rivers (Jensen and Johnsen 1986), where performance is constrained by low temperatures and long winters, and where overwinter habitat (Cunjak *et al*. 1998) might be of paramount importance for survival. In contrast, at the southern range of the distribution, Iberian rivers represent another form of extreme environment, where summer droughts and high water temperatures can impose severe constraints on survival (García de Leániz and Martinez 1988). Thus, it is clear that habitat differences among streams

have the potential for creating local selection pressures (e.g. Riddell *et al.* 1981; Fleming and Gross 1989; Quinn *et al.* 2001a).

Environmental parameters also vary within a context-specific range defined by climatic patterns in continental or temperate zones. Within Europe, the stable seasonal profiles of the Baltic rivers, for example, contrast strongly with those of the British Isles. All these aspects of the physical environment, acting within the context set by predation and competition, can affect performance and have the potential for triggering specialised adaptations among juveniles and adults alike. For example, traits such as egg size, body morphology, run timing or breeding time are affected by water temperature and flow regime (e.g. Jonsson *et al.* 1991a); interpopulation variation, thus, is likely to reflect the outcome of natural selection acting against a background of climatic conditions of varying reliability. In addition to direct effects, temperature can also influence salmon performance indirectly because expression of life histories is tightly linked to temperature-dependent growth variation (Metcalfe 1998).

Following smolting, salmon spend an extended period at sea. Relatively little is known of the routes they take through the ocean (if indeed there are such routes) but the migrations may be extensive since, in the extreme case, fish of southern European origin are represented in fisheries on the western coast of Greenland. On these wide scales, the surface features of the ocean vary markedly, according to latitude and season and according to the dominant, oceanographic patterns of circulation. Both the outward and inward journeys therefore must involve passage through a sequence of marine environments in a manner that is determined in part by population-specific differences in migratory timing, marine routes and speeds of passage, variation which appears to be inherited and which is likely to affect fitness (Kallio-Nyberg and Koljonen 1999; Kallio-Nyberg *et al.* 1999, 2000).

In order to complete their life cycle, therefore, salmon must perform adequately in each of a sequence of disparate environments that fall into several or many main phases, e.g. freshwater growth, transitional migration, marine growth, transitional migration, spawning, embryo incubation and fry dispersal. Performance may be state-dependent and linked among phases (Einum *et al.* 2002; Budy *et al.* 2002). For each phase, the respective environments vary among years and they do so with some independence, tempered by the effect of large-scale climatic forcing processes. Against this background, it is evident that opportunities for selection, and for differential selection among population or regional groupings, are numerous. Constant, stabilising selection is expected to result from the more stable features (e.g. latitudinal effects operating over centuries) of the environmental sequence that fish must transit before reproduction. In addition, however, selection will also occur from environmental variation operating on shorter (decadal) time scales or from challenges that operate intermittently. Selective pressures, hence, may be expected to operate over a wide range of different spatial and temporal scales.

7.2.3 *Reproductive isolation*

Local adaptations can only develop if populations are isolated to some extent, since a substantial exchange of spawners would otherwise tend to homogenise any genetic differences resulting from local selective pressures (Holt and Gomulkiewicz 1997; Lenormand 2002). Reproductive isolation in salmonids is generally high and favoured by strong homing behaviour (reviewed by Stabell 1984; Quinn 1993). However, compared to resident fish, the scope for local adaptations among anadromous salmonids appears to be less extensive (Utter 2001),

possibly because migration and anadromy tend to facilitate gene flow (Gyllensten 1985), while the common marine environment and a complex life cycle may impose a limit to excessive specialisation (Morán 1994; Nicieza 1995).

Nevertheless, homing accuracy in wild Atlantic salmon typically lies in the range 94–98% (Stabell 1984; Youngson *et al*. 1994; Altukhov *et al*. 2000; Jonsson *et al*. 2003), though it may vary between populations (Quinn 1993) and also between wild and hatchery-reared fish (Jóhannsson *et al*. 1998; Jonsson *et al*. 2003). Some degree of straying probably occurs in all salmon populations (Elo 1993; Jonsson *et al*. 2003), although it may not always result in gene flow, due to differences in survival (Borgstrøm *et al*. 2002), reproductive success (Tallman and Healey 1994) or in the timing of breeding (e.g. Quinn *et al*. 2000) of native and foreign fish. Gene flow, hence, may be an order of magnitude less than physical straying (Altukhov *et al*. 2000), although this is still a subject of considerable controversy (e.g. Howard *et al*. 2001; Hendry 2001) as it is difficult to obtain accurate estimates of asymmetric gene flow (but see Consuegra *et al*. 2005b).

The degree of iteroparity in salmon (i.e. the number of times an individual reproduces in a lifetime) is generally small (Jonsson *et al*. 1991a; Altukhov *et al*. 2000), and further restricts the possibilities for dispersing genes to other populations. Repeat spawners, moreover, tend to show very high homing accuracy (Foster and Schom 1989). Thus, homing behaviour, coupled with a tendency to reproduce only once or a few times, and the ability to become sexually mature without a marine phase (especially in males), facilitates the evolution and maintenance of population-specific traits (Hasler and Scholz 1983; Quinn and Dittman 1990).

Nevertheless, genetic evidence for reproductive isolation in Atlantic salmon is still equivocal, which is perhaps surprising considering the observed extent and scale of population structuring (Chapter 5). In general there is no consistent relationship between genetic differentiation at selectively neutral loci and geographical distance between Atlantic salmon populations (King *et al*. 2000, 2001), except when comparisons are made between major groups or lineages separated by hundreds or thousands of kilometres (Elo 1993; Fontaine *et al*. 1997; but see Spidle *et al*. 2003 and Chapter 5). Such lack of concordance between genetic and geographic distances at small spatial scales suggests that genetic drift is high relative to gene flow and/or that there is differential selection (or that the pattern of gene flow does not conform to a stepping-stone model which is counter to results from physical tagging studies: Stabell 1984). Therefore, the evidence from molecular markers also suggests that restricted gene flow among Atlantic salmon populations provides the necessary conditions for local adaptations to exist (Verspoor *et al*. 2002).

7.3 Evidence for the existence of local adaptations in Atlantic salmon

Atlantic salmon populations are, as we have seen, excellent candidates to show local adaptations as they seem to meet the three necessary conditions suggested by Allendorf and Waples (1996): (1) many of the life-history, morphological and behavioural traits that are important for fitness show significant genetic variation both within and among populations; (2) environmental variation among streams is extensive and has the potential for creating local selection pressures; and (3) populations are to a large extent reproductively isolated. Thus, ecological differences among streams, combined with restricted gene flow among populations, provide ample opportunities for population-specific differences to evolve. Yet the extent and

significance of local adaptations in salmonids has been called into question by some (Bentsen 1994; Adkison 1995). When testing for local adaptations, it seems, the debate is not whether the *necessary* conditions are fulfilled, but whether the data are *sufficient* (Endler 1986; McPeek 1997), as we shall examine next.

7.3.1 Indirect, circumstantial evidence for local adaptations

Indirect evidence for the existence of local adaptations in Atlantic salmon is provided by studies of geographical variation in important, fitness-related traits (ecological correlates), by examining clines in genetic variation along environmental gradients, from the translocation of populations outside their native range, and by comparing the relative performance of wild and domesticated fish under relaxed or altered selective regimes (e.g. domestication). Additionally, it is becoming increasingly clear that the Atlantic salmon is not really that much different from other salmonids (Fleming 1998; Hendry and Stearns 2004; Quinn 2005). Thus, the substantial body of evidence that points to the existence of local adaptations in Pacific salmon (e.g. Taylor 1990; Blair *et al.* 1993; Hendry and Quinn 1997; Quinn 2004, 2005) and brown trout (e.g. Elliott 1994; Jonsson *et al.* 1994; Pakkasmaa and Piironen 2001a; Hansen *et al.* 2002) is probably also relevant to Atlantic salmon and should not be ignored.

Ecological correlates in fitness-related traits
Ecological correlates of phenotypic variation along environmental gradients provide one of the most common (albeit least powerful) methods for inferring the existence of local adaptations (Endler 1986). Thus, it is frequently suggested that phenotypic differences among Atlantic salmon populations are associated with variation in local environmental conditions (Youngson *et al.* 2003), often on a clinal basis, but few direct tests of those associations have been reported. Such direct tests generally require reciprocal transfers of individuals between sites or raising of fish from different populations in a common environment in order to identify heritable variation isolated from environmental variation (see below). In Atlantic salmon two types of phenotypic traits have been extensively studied using ecological correlates: variation in body morphology and variation in life-history traits (reviewed by Taylor 1991).

Differences in meristic and morphometric characters found in natural populations of Atlantic salmon (e.g. Thorpe and Mitchell 1981; Reddin *et al.* 1987, 1988; MacCrimmon and Claytor 1985, 1986) have been inferred to be adaptive in many cases. For example, a relationship appears to exist between water velocity and body shape in Atlantic salmon (Claytor *et al.* 1991) and also in pink (Beacham 1985) and coho salmon (Taylor and MacPhail 1985), and this may represent an adaptive response to water flow. Fish with longer heads and more streamlined bodies tend to predominate in high gradient rivers with higher water velocities (Riddell and Leggett, 1981; Riddell *et al.* 1981, Claytor *et al.* 1991). Such morphological variation was confirmed to be heritable by breeding experiments, for differences among Atlantic salmon populations persisted when fish were reared in the same environment (i.e. Riddell *et al.* 1981). In addition, the degree of phenotypic plasticity in shape appears to be high in juvenile salmonids experimentally reared in fast- or slow-flowing waters (Pakkasmaa and Piironen 2001b). Morphological variation in juvenile salmonids is thought to represent an adaptation to local environmental conditions (Riddell *et al.* 1981; Pakkasmaa and Piironen 2001a,b) as morphological differences between populations remain evident among returning adults (e.g. for coho salmon, Fleming *et al.* 1994; Fleming and Gross 1989; for sockeye, Blair *et al.* 1993),

even if juvenile morphologies converge at smolting in preparation for the more homogeneous marine environment (Nicieza 1995).

Atlantic salmon can differ greatly with respect to important life-history traits such as age and size at maturity, reproductive investment (including egg size), age and size-specific survival and longevity (Thorpe and Stradmeyer 1995), not only among populations (Metcalfe and Thorpe 1990; Jonsson *et al*. 1991a; Hutchings and Jones 1998), but also within populations (Myers *et al*. 1986; Jonsson *et al*. 1996; Fleming 1998; Good *et al*. 2001). For example, the age at maturity may vary from a few months in mature parr at the southern end of the range to 10 or more years in large anadromous fish at the northern extreme (reviewed in Schaffer and Elson 1975; Gardner 1976; Hutchings and Jones 1998; see Chapter 2). Mature male parr that may be 1000 times smaller in weight than anadromous males also differ in the pattern of energy allocation, life-history traits and fertilisation success (Thomaz *et al*. 1997; Garant *et al*. 2002; Whalen and Parrish 1999; Arndt 2000; Letcher and Gries 2003).

Several studies indicate that age at maturity is partially inherited in Atlantic salmon (Nævdal 1983; Gjerde 1984). For example, Jonasson (2002) noted that differences in grilse rates between wild populations were maintained when fish were raised in a common environment and that in sea ranching the heritability for grilse rate could be as high as 0.65%. Estimates of heritability for age at maturity of different stocks of Atlantic salmon vary between 0.05 and 0.10 (Holm and Nævdal 1978; see Box 7.3), although heritability values are environment-specific and 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 age at maturity. For example, significant differences in grilse rates between artificial and natural conditions could be the result of the environmental differences and sea growth experienced by post-smolts (Saunders *et al*. 1983; Friedland *et al*. 1996) and sea age can be manipulated by altering ration levels in the preceding winter (Thorpe *et al*. 1990; Reimers *et al*. (1993).

The expression of early maturation in male parr appears to be inherited, but it also depends on attaining a certain body size threshold or growth during development (Prévost *et al*. 1992; Hutchings and Myers 1994; Gross 1996; Whalen and Parrish 1999; Aubin-Horth and Dodson 2004). Each male, hence, has the capability of becoming sexually mature as a parr, but the size threshold for maturation (or some other measure of status, e.g. energy at a given time, Thorpe 1986; Thorpe *et al*. 1998) also appears to be genetically determined and varies among individuals and populations (Aubin-Horth and Dodson 2004). This suggests that there is a significant $G \times E$ interaction for age at maturity in Atlantic salmon, since different populations (genotypes) perform differently in different environments (see Hutchings 2004). Body size, growth efficiency, growth rate, survival and resistance to sea lice infections are also traits for which there is evidence of $G \times E$ interactions in salmon (Table 7.1).

Timing of hatching (Donaghy and Verspoor 1997), embryo muscle development (Johnston *et al*. 2000) and embryo mortality due to low pH (Donaghy and Verspoor 1997) are also heritable in Atlantic salmon, and trait values for different populations are generally consistent with hypotheses of stabilising selection under local environmental conditions. Analysis of post-hatch growth rates suggests that heritable rate differences are not found on small spatial scales (i.e. between tributaries within river systems) (Riddell *et al*. 1981; Johnston *et al*. 2000), but are apparent at larger spatial scales (Nicieza *et al*. 1994a; Jonsson *et al*. 2001). In summary, although associations between phenotypic and environmental variation have not always been easy to interpret, the combined evidence from ecological correlates of important,

fitness-related traits suggests that natural selection (and therefore adaptation) probably plays an important, diversifying role in creating and maintaining phenotypic variation among salmonid populations (e.g. Koskinen *et al.* 2002). Furthermore, the detection of $G \times E$ interactions for many of these traits means that no single genotype can consistently perform best across all environments, thus providing the necessary (albeit insufficient) conditions for local adaptations to develop. Such results also suggest that Atlantic salmon populations differ not only in allelic frequencies at quantitative trait loci, but also in the way those loci interact.

Clines in genetic variation along environmental gradients

The clinal distribution of some allozyme loci or other non-neutral genetic variants along environmental gradients may be indicative of local adaptations (e.g. Crawford and Powers 1989; Powers 1990; Powers *et al.* 1991). In Atlantic salmon, the malic enzyme locus (*MEP-2**) provides the best circumstantial evidence based on allozymes in support of an adaptive cline (reviewed by Verspoor *et al.* 2005). *MEP-2** allelic distribution in Atlantic salmon forms a latitudinal cline in both Europe and North America (Verspoor and Jordan 1989) and populations inhabiting warm rivers tend to show higher frequencies of the *MEP-2* 100* allele than populations living in cold rivers, which tend to show higher frequencies of the alternative (**125*) allele. Significant differences in *MEP-2** frequencies are also observed among populations within river systems (Verspoor and Jordan 1989; Verspoor *et al.* 1991) and seem to be maintained by natural selection (Verspoor *et al.* 1991; Jordan *et al.* 1997), apparently in relation to juvenile growth (Jordan and Youngson 1991; Gilbey *et al.* 1999) and age at maturity (Jordan *et al.* 1990; Consuegra *et al.* 2005a). Thus, genetic variation at the malic enzyme locus seems probably adaptive and the observed differences among salmon populations may reflect local adaptations to different thermal regimes.

Performance of translocated populations

While successful transplantations of salmonids, including Atlantic salmon, have been reported all over the world (Kinnison *et al.* 1998; Quinn *et al.* 1998, 2001b; Cross 2000; Elliot and Reilly 2003), unsuccessful translocations have generally gone unnoticed making any comparative assessment difficult (Mills 1989; Youngson *et al.* 2003). In those instances where it has been possible to carry out a comparative assessment in natural conditions, foreign Atlantic salmon populations did not tend to survive as well as native fish (García de Leániz *et al.* 1989; García-Vázquez *et al.* 1991; Morán *et al.* 1994; Crozier *et al.* 1997; Verspoor and García de Leániz 1997).

Although the failure of transplanted stocks may indicate maladaptation (Altukhov *et al.* 2000), it is usually difficult to rule out alternative explanations. For example, failure of transplanted stocks may result from inferior performance due to hatchery rearing (Einum and Fleming 2001; Jutila *et al.* 2003a, see below). Moreover, such transfers are almost invariably carried out in only one direction (i.e. they are not *reciprocal*). Secondly, the transfer act itself may impair the performance of the transplanted population, especially if only one generation is examined, or if maternal effects carry over multiple generations (Mousseau 2000). Finally, for territorial salmonids such as Atlantic salmon, failure of the translocated stock (even wild fish) may simply reflect the superior competitive ability of residents, rather than the maladaptation of immigrants. For example, only one day of prior residency seems to be enough to provide Atlantic salmon half-sibs with a significant competitive advantage in territorial disputes (Huntingford and García de Leániz 1997). Thus failure of transplanted stocks, however

compelling, should always be viewed with caution when used to support the existence of local adaptation.

Relative performance of wild and domesticated stocks

Since domestication involves an alteration or relaxation of natural selective pressures, the comparative analysis of wild and domesticated populations may provide some insights into the genetic basis of adaptation (e.g. Cruz and Wiley 1989; Shabalina *et al*. 1997).

Compared to wild conspecifics, hatchery-reared fish generally survive worse and stray more (Jonsson *et al*. 2003; Jutila *et al*. 2003a,b), but why? Domestication can greatly affect the body shape of Atlantic salmon (Kazakov and Semenova 1986; Salmanov 1986, 1989; Fleming 1994; Petersson *et al*. 1996). Compared to wild fish, cultured salmon are usually fed in excess and live in a low-exercise environment subject to artificial selection. Morphological responses to culture conditions include reductions in head size, fin length and caudal peduncle height (Fleming *et al*. 1994; Pelis and McCormick 2003), i.e. domestication affects those characters that show the highest level of inter-population variability in natural populations. Similar changes attributable to artificial rearing are also observed in other salmonid species (Taylor 1986; Swain *et al*. 1991), and are thought to reduce the survival of cultured fish in the wild (Johansson 1981; Jonsson *et al*. 1991b). The reasons for such changes are not well understood; domestication is known to cause physical damage (Pelis and McCormick 2003), but may also alter the normal development process (Fleming *et al*. 1994). Morphological changes due to domestication can occur within a single generation of culture and are also detected among sea-ranched salmon; however, they are particularly evident after several generations of farming. Responses to domestication are mediated by both genetic and environmental factors. Thus, although fin growth tends to be very similar in cultured and wild salmon when reared under similar conditions (probably due to fin regeneration), differences in fin length are still detectable between the two groups (Fleming *et al*. 1994), demonstrating that artificial rearing can result in important evolutionary changes (Petersson *et al*. 1996).

The higher levels of developmental instability (measured as fluctuating asymmetry – i.e. random deviations from perfect symmetry; Lajus *et al*. 2003) generally observed in cultured populations compared to wild conspecifics could be due both to environmental conditions such as high densities or low water quality, and to genetic effects induced by unintentional artificial selection. Maladaptation to the hatchery environment can also cause developmental instability (Vøllestad and Hindar 1997). Selection against asymmetric individuals in the wild, and thus decreased fluctuating symmetry in wild populations, has also been considered (Morán *et al*. 1997). Hatchery-reared Atlantic salmon tend to display a high degree of total phenotypic variance compared to wild fish (Salmanov 1986, 1989), possibly due to a higher degree of developmental instability. Cultured populations tend to be more asymmetrical than wild conspecifics (Kazakov *et al*. 1989; Morán *et al*. 1997), perhaps reflecting the more stressful conditions of the hatchery environment. However, other studies (Vøllestad and Hindar 1997; Lajus, unpubl.) found this to be true only in some cases. Another manifestation of developmental instability, the increased frequency of morphological abnormalities such as deformities in the jaw or the operculum, is also more common in cultured Atlantic salmon (Sadler *et al*. 2001 and references therein).

In brief, evidence from the culture of Atlantic salmon indicates that there are a wide number of morphological, behavioural and life-history changes associated with domestication. Changes in body morphology and in behaviour (notably an increase in aggression) are generally the

traits that diverge the most following an alteration/relaxation of natural selective pressures. This suggests that local adaptations (or conversely, maladaptation) are probably related to phenotypic variation in morphology and behaviour, and thus that they may be widespread.

7.3.2 Direct evidence for local adaptations

Unlike the large body of circumstantial, indirect evidence that we examined before, direct evidence indicative of local adaptations in Atlantic salmon is still scant; it comes mostly from two sources: a few, carefully controlled experiments carried out in the field, and the pattern of inherited resistance to parasites and diseases observed in some populations.

Common garden experiments

In a 'common garden experiment', populations from different geographical locations are reared in a common environment, ideally for several generations (Reznick and Travis 2001), and are then tested for phenotypic differences. Since the environment is the same, any phenotypic differences among populations are presumed to reflect genetic differentiation (Mousseau 2000). Despite their apparent simplicity and potential explanatory power, common garden experiments have weaknesses as well, although these can be partially overcome by conducting the experiments in the wild rather than in the laboratory (Endler 1986; Mousseau 2000). Common garden studies, however, are notoriously difficult to carry out in the field and, not surprisingly, few have been undertaken with salmonids. One notable exception includes the large-scale study undertaken in the Burrishoole system (McGinnity *et al.* 1997, 2003), where the freshwater performance of wild, farmed and hybrid progeny of Atlantic salmon was compared in three cohorts, involving both local and foreign populations. No significant differences in survival were found in the hatchery, but there were pronounced differences in survival, growth, downstream movement, parr maturity and smolt age among groups in the field, indicating a genetic basis for these traits. Compared to the wild native population, all other groups (except the progeny of ranched fish) showed consistently poorer survival and produced fewer smolts. Adult return rates and overall lifetime survival were also higher for the native wild population than for most other groups, including wild fish from an adjacent river only a few kilometres away (see Chapter 12).

In another common garden study (García de Leániz, unpubl.), the freshwater performance of juvenile Atlantic salmon from southern (Spain; R. Ulla) and northern (Scotland, R. Shin and R. Oykel) populations was examined in stream tanks and under natural conditions in Spain over two consecutive years. Foreign Scottish ova were identified by a unique mtDNA marker and were temperature-accelerated to mimic developmental conditions in Spain and to ensure near-synchronous hatching. No difference in survival was observed under hatchery conditions. However, under natural conditions, Scottish alevins emerged earlier, had more yolk sac left, grew twice as fast, but had 1.5 times lower survival than native fish 3 months after hatching. At the end of their first year, smolt production was between 1.8 and 9.0 times higher for the native Spanish stock than for the two foreign Scottish stocks. Mean smolt age was also significantly lower for the Scottish stocks (which grew faster) than for the native Spanish stock. Thus, the results of this study indicate that northern salmon populations transplanted into southern rivers survived poorly, despite their superior growth performance.

Similarly, when eyed eggs of two Scottish populations (rivers Oykel and Shin) were planted together in a common garden experiment and their performance monitored both in the field

and in the hatchery, embryo survival under low pH was found to be much greater in the native Oykel stock (subjected to recurrent problems of acidification) than in the foreign Shin population (Donaghy and Verspoor 1997).

Taken together, the results of a few carefully controlled field experiments strongly suggest that native Atlantic salmon performed better because they were locally adapted, though the nature of the local adaptations (i.e. what they were adapted to) is not always known. Reciprocal transfers (whereby native and foreign populations are reciprocally translocated) constitute an even stronger experimental way of testing for local adaptations (Endler 1986; Mousseau 2000). No such test seems to have been undertaken with Atlantic salmon, but experiments with Pacific salmon reveal the superior performance of local fish (e.g. Mayama *et al.* 1989) and the rapidity with which such evolution can occur (Unwin *et al.* 2003).

Inherited resistance to parasites and diseases

The geographical pattern of inherited resistance to the external monogenean parasite, *Gyrodactylus salaris*, constitutes probably the most convincing example of local adaptation in Atlantic salmon (see Box 7.4). Comparative phylogenies of Atlantic salmon and *Gyrodactylus salaris* suggest that *G. salaris* was originally a parasite of grayling 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. Currently, Baltic populations are generally resistant to infection by *Gyrodactylus salaris* whereas salmon populations migrating into the Atlantic are generally susceptible or partially susceptible to the parasite (Bakke and MacKenzie 1993; Rintamäki-Kinnunen and Valtonen 1996; Bakke *et al.* 2002; Dalgaard *et al.* 2003).

Other recent studies suggest that parasite-mediated balancing selection may drive genetic variation at the major histocompatibility complex (MHC; Consuegra *et al.* 2005c,d), and result in local adaptations with respect to pathogen resistance in Atlantic salmon and other fishes (Landry and Bernatchez 2001; Langefors *et al.* 2001; Lohm *et al.* 2002; Bernatchez and Landry 2003; Wegner *et al.* 2003).

7.3.3 Challenges to the local adaptation hypothesis

Although the prevailing view today, just as it was in 1991 when Taylor reviewed the subject, is that salmonid populations are locally adapted, the local adaptation hypothesis continues to be challenged (e.g. Bentsen 1994; Adkinson 1995). The following four questions are often raised.

(1) If salmon populations are indeed locally adapted, how is it that most of the observed genetic variation is within populations, rather than among populations?

In other words, most of the genetic differences are between individual fish, not between fish from different populations. Furthermore, why is most of the genetic variation observed among populations due to differences in allele frequencies, rather than to the occurrence of unique, private alleles in each population?

From the perspective of quantitative genetics theory, the above observations would imply that salmon populations should be largely overlapping in terms of adaptive traits; in other words they should be *universally* rather than *locally* adapted. If so, the mixing of populations might be expected to enhance population fitness. However, what evidence there is suggests the opposite is true: population mixing in Atlantic salmon and other salmonids tends to result in

outbreeding depression and loss of fitness (e.g. Einum and Fleming 1997; McGinnity *et al.* 2003; Hallerman 2003b), thus implying the existence of locally adapted gene complexes.

Admittedly, little is known about the actual molecular basis of adaptive genetic variation in the wild (Mitchell-Olds 1995; Lynch and Walsh 1998), but adaptive differences among populations are certainly not contingent on populations having unique alleles or non-overlapping distributions of phenotypic traits, as shown in Box 7.5.

In only a few cases do the genetics of traits apparently linked to adaptation appear to be simple. For example, variation in coloration in the moth, *Biston betularia*, is determined by a single gene and thought to involve balancing selection, though the actual mechanisms of selection remain unclear (Hartl and Clark 2000; Grant and Grant 2002). A major assumption underpinning classical quantitative genetics theory (Lynch and Walsh 1998) is that most quantitative traits are controlled by many genes (i.e. they are polygenic). To what extent this is true is unknown. Certainly, modelling suggests that the continuous distributions observed for quantitative traits can arise from variation in as few as two or three genes when 50% of trait variation is due to the environment, and from as few as 12 genes when the influence of the environment is negligible (Tave 1993). Therefore, a high level of genetic variability within populations can neither prove nor disprove the existence of local adaptations.

(2) How can salmon populations be locally adapted and yet sometimes perform so well (and evolve so rapidly) outside their native habitats?

As pointed out before, some of the apparent success of translocated populations must undoubtedly be a result of what has been termed selective memory: only successful translocations tend to be reported, while unsuccessful attempts (and these must have been legion) go quietly unnoticed. Nevertheless, there are many examples of salmonids performing well outside their native habitats, even in such distant places as New Zealand or Australia. How is this possible? It seems that, for salmonids, one consequence of living in highly changing aquatic environments has been the development of considerable phenotypic plasticity (i.e. flexibility), which may itself have been the target of selection (Jørstad and Nævdal 1996; Pakkasmaa and Piironen 2001b). Thus, the same flexibility that may have allowed salmonids to adapt to local environmental conditions may have also allowed them to perform successfully in a variety of aquatic habitats (Klemetsen *et al.* 2003) and to evolve rapidly outside their native range (Hendry *et al.* 2000; Quinn *et al.* 2000, 2001b).

(3) How can migratory salmon adapt locally to an environment that changes so much spatially and temporally?

Although little is known about the patch dynamics of local adaptations in salmonids (what are salmon adapted to?, how long does it take to become adapted?; Rieman and Dunham 2000), genetic differentiation for adaptive behavioural traits can be surprisingly rapid in other organisms (e.g. Cousyn *et al.* 2001), providing a plausible mechanism for evolutionary change. Again, the ability shown by many salmonids to produce different phenotypes in different environments suggests that the costs of phenotypic plasticity are not too great (or that the benefits outweigh the costs; see DeWitt *et al.* 1998). Thus, when the environment is heterogeneous and unpredictable, selection may tend to favour a 'jack of all trades' strategy. It seems likely that the most reliable features of the salmon's niche, such as the temperature regime, the photoperiod, or the occurrence of predators, parasites and diseases, are perhaps the conditions most likely to trigger the development of local adaptations in salmon populations.

(4) If random genetic drift is the overriding diversifying factor in small, isolated populations (typical of many salmonids), then how can local adaptations be maintained under such conditions?

Undoubtedly, many salmon populations are fairly small and may be expected to have lost much genetic variation due to genetic drift (Adkison 1995; Bentsen 2000), unless there is a high level of gene flow (which would then tend to erode any local selective advantage (Holt and Gomulkiewicz 1997; Lenormand 2002). However, the relationship between genetic variation and fitness in salmonids is a complex one (Wang *et al.* 2002a,b), and natural selection seems to be able to create and maintain adaptive phenotypic variation even among surprisingly small salmonid populations (Quinn 1999; Quinn *et al.* 1998, 2001b; Koskinen *et al.* 2002). Moreover, the possible existence of salmonid metapopulations (Fontaine *et al.* 1997; Rieman and Dunham 2000) means that local adaptations can probably persist in spite of some gene flow from adjacent, loosely related neighbours (Hanski 1999). Finally, there may be local adaptation for some traits but not for others.

7.4 Summary and conclusions

- The process of adaptation represents the end product of natural selection and can be viewed as the degree of matching between the phenotype and its environment.
- Local adaptations are revealed when the average performance of local fish exceeds that of immigrants; they evolve when populations are reproductively isolated, live in heterogeneous environments and are subjected to differential selective pressures. Local adaptations are likely to exist in Atlantic salmon, but their extent is probably very variable, depending on habitat heterogeneity and patterns of gene flow.
- Detailed knowledge of environmental variation across the Atlantic salmon range is scant, and this has no doubt hindered the identification of local selective pressures at biologically meaningful scales. Application of new techniques, such as those developed in geostatistics and landscape genetics (Manel *et al.* 2003), should prove useful in identifying the extent of local adaptations in Atlantic salmon.
- Water temperature and photoperiod (and variables related to them) are likely to be among the most important physical variables determining local selective pressures in Atlantic salmon populations. They are also relatively stable and predictable in a way that promotes the development of local adaptations.
- Heritability estimates for many fitness-related traits indicate that growth and body composition have the highest heritabilities among those examined, followed by health condition and resistance to diseases, and survival and life history variation, which have the lowest. G × E interactions are found for many of these traits, again suggesting that local adaptations might be important.
- Inferential evidence for the existence of local adaptations in Atlantic salmon comes from genetic correlates in fitness-related traits, the failure of many translocations, the poor performance of domesticated stocks, the results of common garden experiments, and the pattern of inherited resistance to some parasites in the wild, as well as from research in other salmonid species.
- The best example of a local adaptation in Atlantic salmon is perhaps the inherited resistance to the monogenean external parasite, *Gyrodactylus salaris*, shown by some Baltic

populations but not by populations elsewhere. Many examples of this kind of adaptation are also found in other salmonid species.

- Since maladaptation often results from phenotype–environment mismatching, it becomes important to protect and maintain the native genotypes, as well as the original habitat conditions to which the populations have historically adapted.

7.5 Management recommendations

There is, we have seen, a substantial body of circumstantial evidence that suggests that populations of Atlantic salmon, like those of many other salmonids, are probably locally adapted. There are also some experimental results and certain patterns of inherited resistance to parasites and diseases that can be best viewed as local adaptations. However, what are the practical implications for conservation and management and, more precisely, how is adaptive genetic variation maintained and how is it lost?

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 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 on the genes (Box 7.6, Figs B7.6a and B7.6b) or in the environment (Box 7.6, Figs 7.6c and B7.6d).

Collectively, the evidence suggests that local adaptation is an inevitable consequence of natural selection acting on genetic diversity and phenotypic plasticity in heterogenous habitats. If so, the management of Atlantic salmon should aim to minimise alterations in either the genotype or the environment of populations, while maintaining the conditions necessary for natural selection to operate efficiently and unhindered. This means that salmon populations should ideally be allowed to reach or extend beyond carrying capacity, and that competition and other sources of natural mortality (e.g. predation, diseases) may need to be allowed to develop. Furthermore, a number of specific management recommendations emerge (explored in more detail in chapters of Part III):

- View each breeding unit as largely but not entirely isolated, and manage each unit at the smallest (spatial and temporal) scales possible (i.e. tributaries, 1SW vs MSW, etc.).
- Maintain salmon populations at their largest possible size in order to retain genetic variation and adaptive potential, especially in the case of small populations inhabiting extreme, marginal habitats.
- Stop transplants of non-native fish (unless there is a clear genetic case for doing so), and limit or preferably eliminate aquaculture escapes.
- Critically examine 'supplementation' hatcheries and 'enhancement' programmes, especially the hidden costs of density-dependent competition and swamping of wild gene pools.
- Finally, minimise habitat change and where possible protect and maintain the habitat and natural conditions to which populations have historically adapted.

Box 7.1   Adaptation and fitness in changing environments.

Adaptation can be defined as the good fit of organisms to their environment (Gould and Lewontin 1979). 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 (Fig. B7.1). 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. For example, in the example illustrated below (Fig. B7.1) 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', contained between E_{max} (the upper environmental limit) and E_{min} (the lower environmental limit). Loss of fitness, and eventual extinction, may be expected to occur outside the adaptive zone (see Box 7.6).
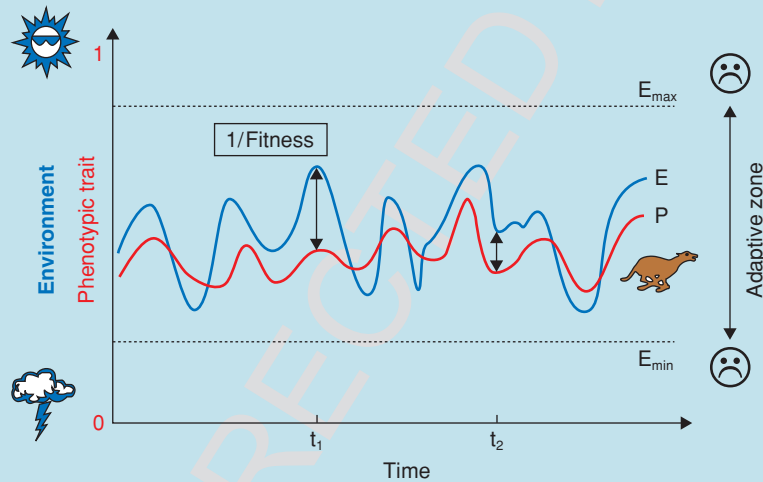

Fig. B7.1   Temporal changes in fitness in changing environments.

Box 7.2   Fisher's two opposing forces of evolution (Fisher 1958).

The fitness of an organism can be viewed as the degree of matching between the phenotype and the environment, being augmented in each generation by natural selection, and eroded by deleterious mutation and environmental change (Fig. B7.2a). As organisms are forever struggling to keep pace with environmental change, they are effectively 'fighting change with change' (Meyers and Bull 2002). Thus, when confronted with a change in environmental conditions of a given intensity and frequency, organisms may be expected to respond by adjusting their phenotype in the present or subsequent generations; the efficiency of such phenotypic adjustment will depend on the organism's adaptability (i.e. the magnitude by which organisms can adjust their phenotypes by evolutionary responses and phenotypic plasticity) and generation time (Fig. B7.2b).
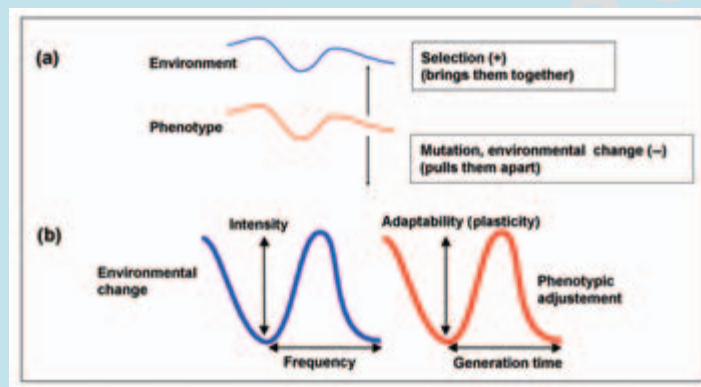
Fig. B7.2   (a) How the two opposing forces of evolution act together to determine fitness. (b) How changes in the environment (determined by their intensity and frequency) are matched by changes in the phenotype (determined by the degree of phenotypic plasticity and the organism's generation time).

Box 7.3   Estimating heritabilities: how much do like beget like?

The variance of the phenotype (i.e. the character we observe) can be partitioned into two components (Fig. B7.3a), one due to the effects of the environment (V_E) and one due to the effects of the genes (V_G); the genetic component of the phenotype is the only one that is passed from parents to offspring. Environmental effects can be subdivided into random (V_{ER}; those we cannot control) and systematic effects (V_{ES}; those we can recognise and control). Likewise, the inherited or genetic component of the phenotype (V_G) can be partitioned into additive and non-additive effects. Non-additive genetic effects represent the action of dominant (V_D) and epistatic (V_I) gene interactions: these change in each generation due to segregation and recombination and are of little predictive value. Additive genetic effects (V_A), on the other hand, are not disrupted in each generation, and represent the combined (additive) effect of multiple genes to the expression of a trait. The ratio of additive genetic variance to the total phenotypic variance is called the heritability (h^2) in the narrow sense (or simply the heritability); it measures how much of the phenotype is likely to resemble that of its parents. The higher the heritability, the more rapid the response to selection is likely to be (Mazer and Damuth 2001). The ratio of the total genetic variance (V_G) to the phenotypic variance is called the heritability in the broad sense (H^2). Although it measures the extent to which the phenotype is determined by the genotype, it is of little predictive value due to the unpredictable interactions of epistatic and dominant genes.

   Most traits for which there are heritability estimates in Atlantic salmon are those that bear some economic significance for the salmon farming industry, in particular those related to growth, health condition and resistance to infectious diseases. Although heritability estimates are always population-specific and context-dependent, those traits related to life history and overall survival have relatively low heritabilities in Atlantic salmon, whereas
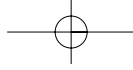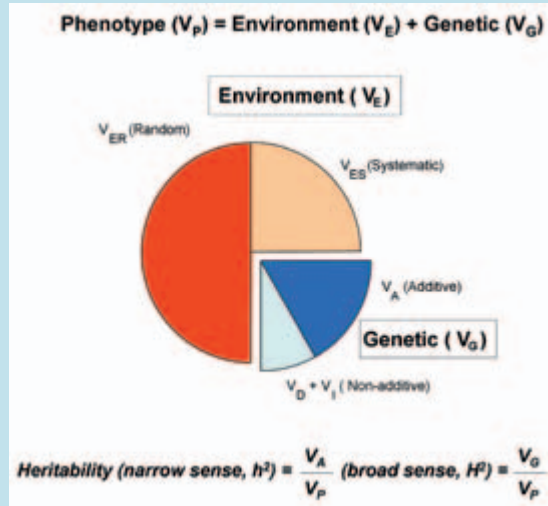
Box 7.3   (*cont'd*)

Fig. B7.3a   Partition of the phenotypic (P) variance into its environmental (E) and genetic (G) components, and definition of the heritability value.
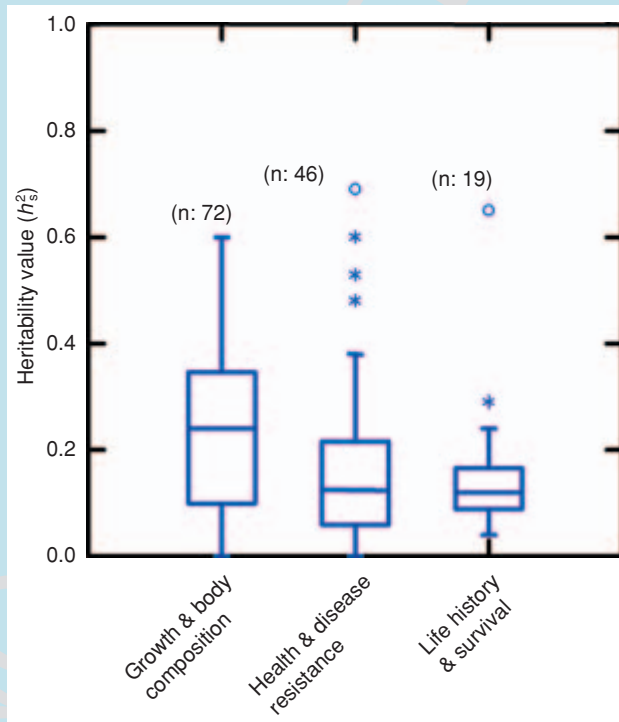

Fig. B7.3b   Heritability estimates for various fitness-related traits in Atlantic salmon grouped by trait class.

those traits related to growth, body size and body composition generally yield higher heritabilities (Fig. B7.3b). Similar results are found in a variety of other organisms, both in laboratory and field conditions (Mousseau and Roff 1987; Hoffman 2000). In general those characters with the lowest heritability may be expected to be the ones most closely related to fitness (Falconer and McKay 1996; Merilä and Sheldon 1999).
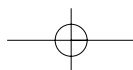
Box 7.4   An example of local adaptation in Atlantic salmon: resistance to the parasite *Gyrodactylus*.

Gyrodactylosis is a fish disease caused by ectoparasitic monogenean flatworms of the genus *Gyrodactylus*. There are thousands of *Gyrodactylus* species in the world (Bakke *et al.* 2002), probably parasitising many fish species in freshwater, brackish and marine environments. These parasites attach to the host surface by means of hooks and feed on epithelial tissue, seldom causing death. Only in special circumstances, the propagation on host gills or skin can escalate and lead to heavy infestation, osmotic stress and secondary infections which may kill the fish, especially during the juvenile stages. Although most members of the genus appear to be host specific, some fish hosts may harbour more than one species of *Gyrodactylus* (Cone 1995), which in the case of *Gyrodactylus salaris* seems to have undergone host switch and rapid adaptive divergence (Meinilä *et al.* 2004). Gyrodactylosis is only one among the many infectious diseases of salmon but together with myxozoans, furunculosis and sea lice it is most likely to threaten wild and farmed salmon stocks in the future (Bakke and Harris 1998).

   Resistance to *Gyrodactylus salaris* constitutes a classic example of local adaptation in salmonids and 'how a presumed harmless organism may become a pathogen if it is introduced to new areas where the host lacks effective responses against it' (Mo 1994). It is believed that *G. salaris* was probably introduced to Norwegian waters in the 1970s with infected salmon imported from a hatchery in Sweden (Johnsen and Jensen 1986, 1991; Bakke *et al.* 1990; Mo 1994). Within months the parasite spread quickly through the juvenile population and was soon detected in more than 40 salmon rivers, causing considerable damage in both wild and hatchery populations (Lund and Heggberget 1992). Two years after the introduction of *Gyrodactylus salaris*, salmon parr densities decreased by half, and Atlantic salmon became virtually extinct in most infected rivers 5–7 years later (Johnsen and Jensen 1986; Mo 1994). There appears to be no remedial treatment against infection by *Gyrodactylus salaris*, and the only control measure consists of applying rotenone (a poison which eliminates all the fish in the river), followed by stocking with parasite-free salmon stocks (Scholz 1999).

   Atlantic salmon populations in the Baltic appear to be innately resistant to infection by *Gyrodactylus salaris*, whereas Norwegian, Scottish and other salmon populations migrating into the Atlantic are generally susceptible or partially susceptible (Bakke *et al.* 1990, 2002; Bakke 1991; Bakke and MacKenzie 1993; Rintamäki-Kinnunen and Valtonen 1996; Dalgaard *et al.* 2003). Under controlled laboratory conditions the parasite exhibits marked differences in fecundity, development and mortality when it infects different stocks (MacKenzie and Mo 1994; Cable *et al.* 2000), which may explain its variable virulence (Fig. B7.4a).

   Host resistance to the parasite is known to be heritable (Jansen *et al.* 1991; Bakke *et al.* 1999) and probably under polygenic control (Bakke *et al.* 2002). Laboratory experiments have indicated possibly disastrous consequences of introducing *G. salaris* into new areas (MacKenzie and Mo 1994). However, why are salmon populations from the Baltic resistant to *G. salaris* while populations from the Atlantic are susceptible? Recent work on the phylogeography of *Salmo salar* in Europe (Verspoor *et al.* 1999) has shown that there are two distinct genetic lineages since the last ice age – Baltic and Atlantic. Most, if not all, of the Baltic salmon populations are derived from the Upper Volga ice lake (Koljonen *et al.* 1999; Nilsson *et al.* 2001), in contrast to the Atlantic lineage that probably originated from the Iberian Peninsula (Consuegra *et al.* 2002). The phylogeny of *Gyrodactylus* (Fig. B7.4b), on the other hand, suggests that *Gyrodactylus salaris* was originally a parasite of grayling, and 'jumped' to Baltic salmon in the large, Upper Volga ice lake. Although *G. salaris* cannot disperse easily in seawater, it can spread quickly in fresh water and it is likely that the refugial ice lake must have provided ample opportunities for spreading the parasite. During this episode, most salmon from the Baltic basin must have initially become infected, and then gradually acquired resistance due to the effect of natural selection. Salmon populations from the Atlantic lineage, in contrast, were never in contact with the parasite and did not develop resistance.

   Phylogenetic analysis of *Gyrodactylus salaris* in rainbow trout, Atlantic salmon and grayling based on mtDNA sequences (Fig. B7.4b; Meinilä *et al.* 2002, 2004) indicates that there are four independent evolutionary lineages or strains of *Gyrodactylus salaris*. These are, however, not sufficiently differentiated to earn a species rank. One strain is commonly found in rainbow trout farms in Finland, Denmark and Sweden, and also in Norway and Russia. This 'rainbow trout strain' is genetically homogeneous and widely distributed among rainbow trout stocks, which are not harmed. Harm only comes when this parasite infects Atlantic salmon populations outside the Baltic area (Baltic salmon are resistant against the rainbow trout strain of *G. salaris*). The other phylogenetic lineage is the '*Gyrodactylus salaris* proper', the strain described by Malmberg in 1957. It is more variable and is found naturally not only in salmon stocks from the Baltic, but also in many rivers in Norway (e.g. R. Vefsna) and in the White Sea (R. Keret). The fact that Baltic salmon tolerate the Baltic strains of *G. salaris* and that the gyrodactylosis found in the Swedish west coast is 'balanced' and not fatal, suggests that there was some salmon gene flow out from the Baltic (Malmberg and Malmberg 1993). The malign *Gyrodactylus* infections on the Atlantic side and

Box 7.4 (*cont'd*)
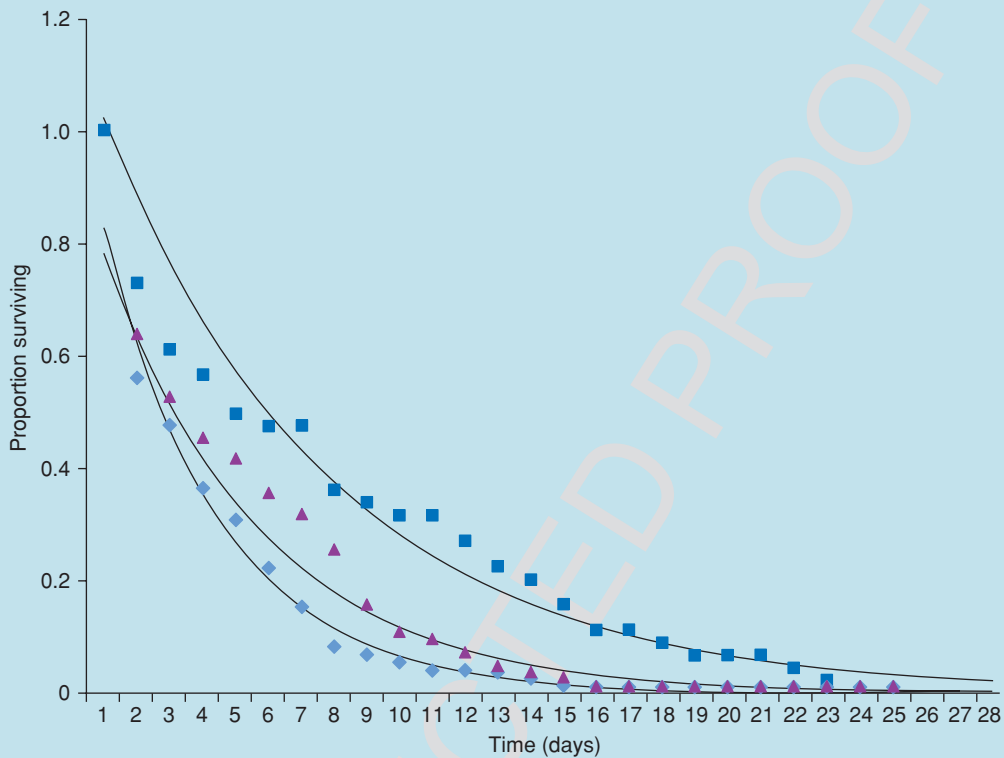
Fig. B7.4a Survivorship curves of *Gyrodactylus salaris* on two susceptible Atlantic salmon stocks from Norway (Alta ■ , Lier ▲) and one resistant stock from the Baltic (Neva, ◆) infected experimentally. Parasite establishment success (proportion of worms surviving to give birth) was significantly lower in the resistant stock (45% with mean parasite survival of 3.5 days) than in the two susceptible stocks (60% with mean parasite survival of 7.9 and 5.2 days, respectively). Source: Cable *et al.* (2000).

the benign ones in Baltic rivers are caused by parasites closely related to each other. Two geographically isolated evolutionary lineages are observed in grayling (*Thymallus thymallus*). One is found in the White Sea basin, and the other in the Baltic basin. The grayling strains are *sister* clades to those infecting salmon and rainbow trout, of similar evolutionary age (~ 150 000 years). The parasite strains detected in grayling appear to be strictly host specific, and do not infect Atlantic salmon in the same rivers (Tornionjoki, Finland/Sweden and Pistojoki, Russia). Norwegian graylings have their own strain, also found to be harmless for Atlantic salmon (Bakke *et al.* 2002; GenBank entries).

Box 7.4   (*cont'd*)
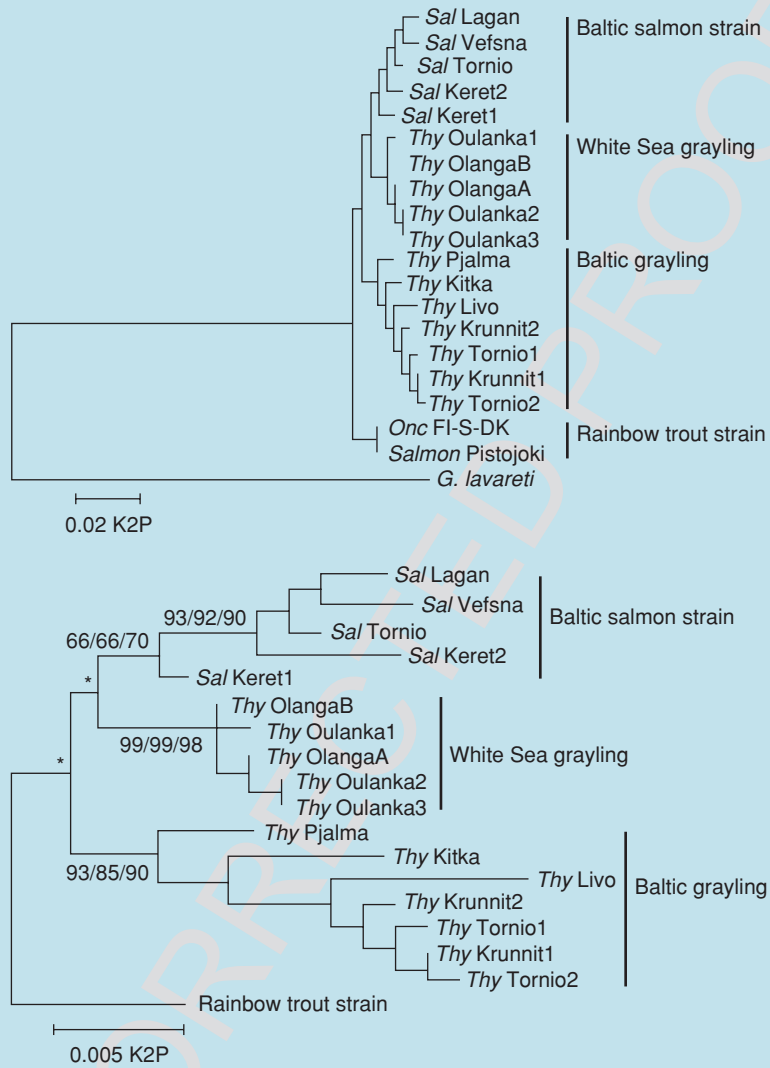
Fig. B7.4b   Phylogenetic analysis of *Gyrodactylus salaris* in rainbow trout, Atlantic salmon and grayling based on mtDNA sequences. (upper) Tree 'rooted' with nearest relative *Gyrodactylus lavareti*. (lower) Only *G. salaris* clones. Based on sequencing about 800 bp of the mitochondrial gene *COI*; the scale is Kimura's two parameter distance (K2P) and the numbers along branches indicate the statistical significance (%) of each branch, achieved by different tree-building methods. Source: Meinilä *et al*. (2004).

Box 7.5   Can allele frequency differences underlie phenotypic divergence?

The genetic requirements for local adaptation of populations are largely unknown and likely to be highly variable depending on the trait involved. However, adaptive genetic differentiation between populations for phenotypic traits which show both within- and between-population variation as commonly observed can, in principle as least, arise where genetic differences are solely generated by differences in allele frequencies, as the following hypothetical example shows. The two populations shown differ in mean gill raker number (Fig. B7.5a), a trait for which variation is known to be associated with different diets and whose variation can be both genetically and environmentally determined. These phenotypic distributions can be generated by genetic variation at three loci, each with two alleles, where trait heritability is 0.46, i.e. 46% of variation among individuals is genetic. In this model, the effect is additive. For each copy of allele p possessed by an individual at each locus it develops one gill raker while for each copy of allele q it generates two. Thus the genetically determined number of gill rakers can range from 6 (i.e. 6 copies of p – two at each locus) to 12 (i.e. 6 copies of q). The model also assumes that the actual distribution of phenotypes for a given genotype varies around the genotype value by two rakers due to the effect of the environment as shown below, with 50% of individuals having the type dictated by their genotype (Fig. B7.5b).

In this model, the phenotype distributions can be generated if the allele frequencies in population 1 are $p = 0.8$ and $q = 0.2$ at each of the three loci, and $p = 0.2$ and $q = 0.8$ at each locus in population 2. This gives the genotypic distributions shown below for the two populations (Fig. B7.5c).

All genotypes can occur in each population but expected frequencies in the populations are highly divergent: for example, the most common genotype in population 1, genotype 1, is expected to be possessed by over 25% of individuals in population 1 but by less than 0.01% of fish in population 2. The converse would be true for genotype 27. If each population has 1000 fish, 852 of the fish in each population would be expected to be of five genotypes which would be represented on average by less than two fish in the other population. This allele frequency divergence could be maintained, under certain conditions, by selection favouring individuals in each population which possess the mean gill raker number for that population.
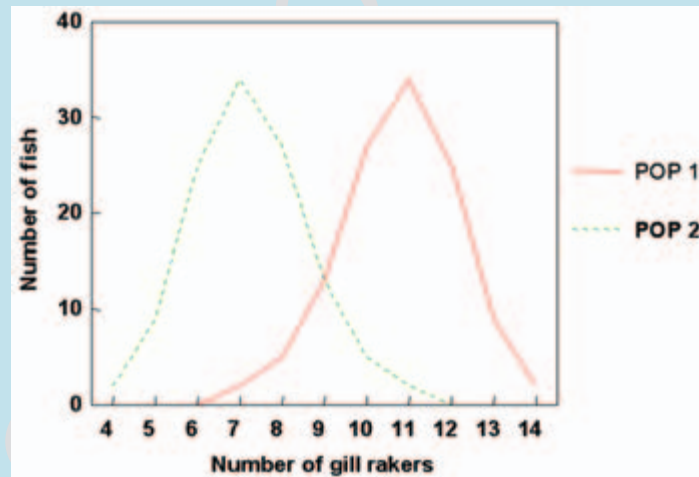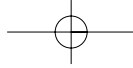

Fig. B7.5a   Hypothetical distribution in the number of gill rakers in two salmon populations, a trait whose variation can be both genetically and environmentally determined.
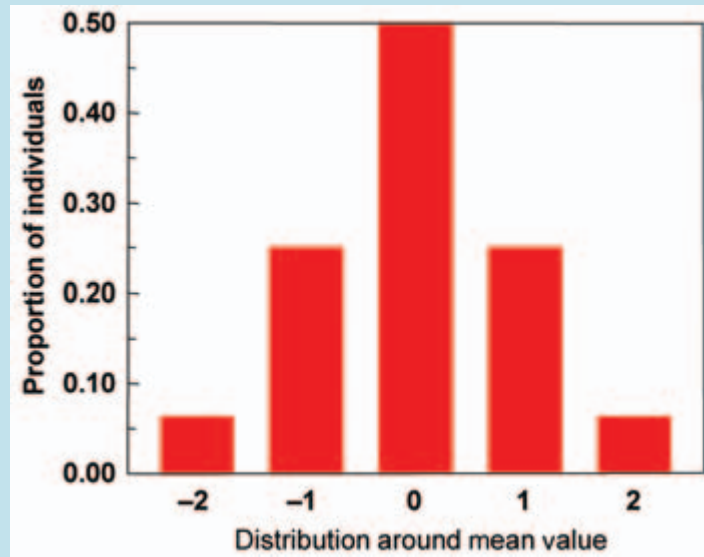
Box 7.5   (*cont'd*)

Fig. B7.5b   Hypothetical degree of phenotypic variation in the number of gill rakers around the mean value for a given genotype due to environmental effects.
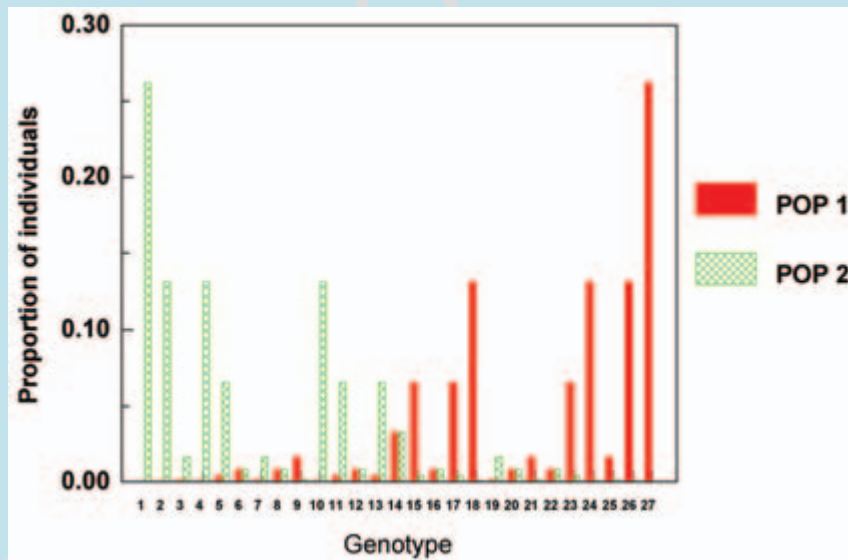

Fig. B7.5c   Resulting distribution of genotypes when the phenotypic distributions in gill raker number are generated by genetic variation at three loci, each with two alleles, and a trait heritability of 0.46. The model assumes additive genetic variation. For each copy of allele *p* possessed by an individual at each locus it develops one gill raker while for each copy of allele *q* it generates two.
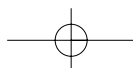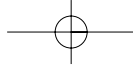
**Box 7.6** Four ways to lose adaptive variation and fitness.

Problem 1

Loss of fitness, and eventual extinction, may occur if the genotype (and thus likely the phenotype) is allowed to shift 'out of bounds', i.e. outside the adaptive zone defined by the optimal environment for the population (Fig B7.6a). Such a situation could happen through random genetic drift (random loss of alleles) following a severe decline in population size, gene swamping or gene introgression due to stocking with maladapted individuals, or selective exploitation. In this example, the phenotype (P) first shifts beyond the adaptive zone at time t_c.
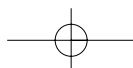
Problem 2

Loss of genetic variation may result in loss of fitness if it makes the population more vulnerable to environmental change. In this second example (Fig. B7.6b), changes in the genotype at time t_c result in a subsequent reduction in the population's tolerance limits, thereby reducing its ability to cope with future environmental changes and increasing the risk of extinction. Such a scenario is typical of small, bottlenecked populations following severe reductions in population size (see Chapter 9).
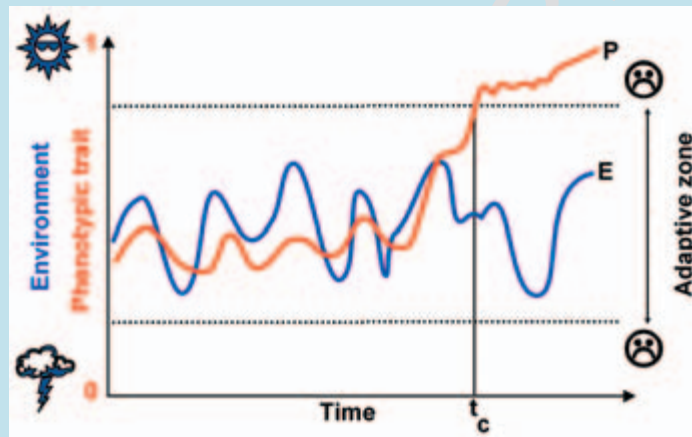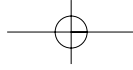

Fig. B7.6a Problem 1. Phenotype/genotype shifts beyond the adaptive zone.
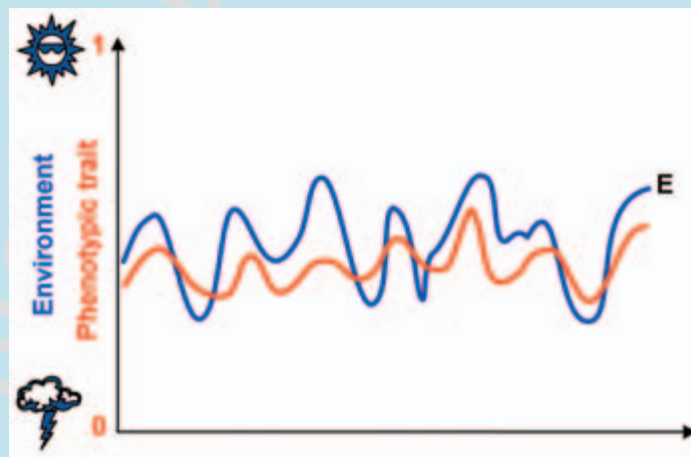
Fig. B7.6b Problem 2. Loss of genetic variation.

Box 7.6 (*cont'd*)

Problem 3

Just as the genotype can shift outside the adaptive zone in the preceding example (problem 1), loss of fitness can also occur if the environment (rather than the genotype) is the one that goes 'out of bounds', i.e. beyond the adaptive zone defined by the historical environment for the population (Fig. B7.6c). Such a condition could develop, for example, when key habitats are destroyed or the environment is altered beyond the population's tolerance limits.

Problem 4

The population may also fail to adapt if the environment (E) begins to change too rapidly in relation to the population's phenotypic plasticity (P) (Fig. B7.6d), which will always depend on generation time. Examples of rapid environmental changes include the sudden discharge of some power stations, and those brought about by deforestation, impoundment and stream regulation, siltation, point-source pollution, or blockage of migratory routes. Other, less rapid sources of enviromental change may include climate change (Carpenter *et al.* 1992).
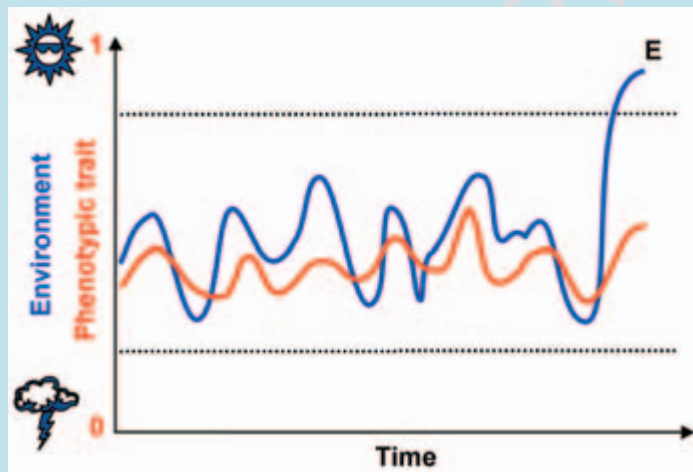

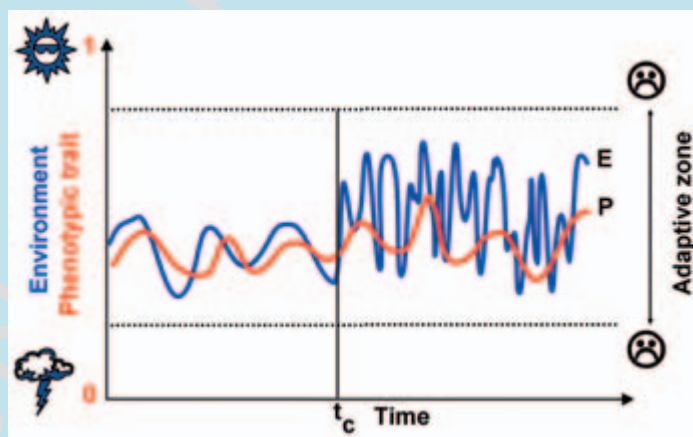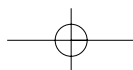**Fig. B7.6c** Problem 3. The environment changes too much.

Fig. B7.6d Problem 4. The environment changes too quickly.

Acknowledgements

We are most grateful to Hans Bentsen for compiling most of the data on heritability values in Atlantic salmon and for pointing out some of the problems with the local adaptation hypothesis, and to J. Lumme, J. Kuusela and M. Meinilä for kindly providing the information in Box 7.4 and most of the information on adaptation to *Gyrodactylus*. Their help was invaluable and is gratefully acknowledged.

Further reading

There are many specialised texts dealing with the subject of adaptation and natural selection, but few are easy to follow. Some of the most accessible are listed below:

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Mayr, E. (2002) *What Evolution Is*. Phoenix, London.

Mousseau, T.A.; Sinervo, B. and Endler, J. (Ed.) (2000) *Adaptive Genetic Variation in the Wild*. Oxford University Press, Oxford.

Rose, M.R. and Lauder, G.V. (Ed.) (1996) *Adaptation*. Academic Press, San Diego, CA.

Stearns, S.C. (1992) *The Evolution of Life Histories*. Oxford University Press, Oxford.

For a different (and provocative) look at adaptation and natural selection try:

Macbeth, N. (1971) *Darwin Retried: An appeal to reason*. Gambit, Boston, MA.

For local adaptations in salmonids see:

Altukhov, Y.P.; Salmenkova, E.A. and Omelchenko, V.T. (2000) *Salmonid Fishes: Population biology, genetics, and management*. Blackwell Science, Oxford.

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