



ELSEVIER

Fisheries Research 62 (2003) 193–209

**FISHERIES  
RESEARCH**

www.elsevier.com/locate/fishes

# Management of salmonid fisheries in the British Isles: towards a practical approach based on population genetics

A.F. Youngson<sup>a,\*</sup>, W.C. Jordan<sup>b</sup>, E. Verspoor<sup>c</sup>,  
P. McGinnity<sup>d</sup>, T. Cross<sup>e</sup>, A. Ferguson<sup>f</sup>

<sup>a</sup> FRS Freshwater Laboratory, Faskally, Pitlochry, Perthshire PH16 5LB, UK

<sup>b</sup> Institute of Zoology, Regent's Park, London, UK

<sup>c</sup> FRS Marine Laboratory, Aberdeen, UK

<sup>d</sup> Marine Institute, Newport, Ireland

<sup>e</sup> National University of Ireland, Cork, Ireland

<sup>f</sup> The Queen's University of Belfast, Belfast, Northern Ireland, UK

## Abstract

The evidence for structuring of Atlantic salmon (*Salmo salar*) and brown trout (*Salmo trutta*) into distinct reproductive populations and for genetic differentiation and local adaptation is compelling. The effect of genetic variation among populations is demonstrably a factor determining the economic value of salmonid fisheries in the British Isles. Genetic considerations are, therefore, a matter of self-interest for fisheries managers and a shared interest with those advocating more general approaches to the conservation of diversity and variation. The local population is the basic unit of production and, therefore, the preferred unit of management. However, salmonid populations are numerous and many are small. These factors limit practical possibilities for management at the population level. We suggest that this difficulty can be addressed by combining populations in fisheries-biased management units that comprise interchangeable, nested groupings of populations that are both genetically and biologically meaningful. This population-based approach addresses the necessity of managing the fisheries in ways that are consistent with the conservation of adaptive potential in relation to the dynamic aspects of populations, their capacity to respond to changing environmental conditions, and the likelihood that salmonids will remain a worthwhile resource for the future.

Crown Copyright © 2002 Published by Elsevier Science B.V. All rights reserved.

*Keywords:* *Salmo salar*; *Salmo trutta*; Genetics; Population; Conservation; Fisheries management

## 1. Introduction

Atlantic salmon (*Salmo salar* L.) and brown trout (*Salmo trutta* L.) have been integral parts of the natural biodiversity of the freshwater ecosystems of temperate and sub-arctic regions bordering the north-

east Atlantic, since rivers, lakes and streams took their present form in the aftermath of the last glacial retreat. Both species have probably constituted an important resource for man over most of this same period. Relatively recently, the economic value of the wild resource in the British Isles has come to be dominated by recreational exploitation by angling, rather than, as previously, by food fisheries. However, many salmonid fisheries in the British Isles, as in other parts of the species' range, are in decline

\* Corresponding author. Tel.: +44-1796-472060;

fax: +44-1796-473523.

E-mail address: a.youngson@marlab.ac.uk (A.F. Youngson).

and the value of the recreational fisheries is at risk. In response, the restoration of salmonids to their former, self-sustaining abundance has become one of the primary objectives of fisheries management. There are many potential causes for stock declines and, in some cases, single fisheries are compromised by several effects. Against this background, a range of approaches to restoration has been identified. These are frequently based on hatchery-rearing and restocking and often involve transfer of fish among locations.

The general value of the salmonid resource is determined by attitudes based on philosophical and social factors that relate to diversity and abundance. Society puts separate, high values on the conservation of biodiversity and on angling as a recreational resource. Biodiversity and recreational exploitation are not obviously connected themes. However, they are linked by the biological factors that determine the abundance and variety of salmonids, since these are likely to include genetic factors. This argument can be expanded as follows.

The economic value of recreational fisheries derives from five factors. It is determined by: (1) the abundance of the individuals and (2) the diversity of types that are available for exploitation. In the latter case, for example, only brief seasonal fisheries are possible for Atlantic salmon in some catchments, while in others run-timing variation permits extended fisheries covering most of the months of the year. In the case of brown trout, variation in life-history (i.e. anadromous or freshwater resident) brings variety to local fisheries. The total value of the national fisheries includes the sum of the values of all the local fisheries but additional value is imparted by (3) the overall national abundance of salmonids and (4) their overall diversity. The former term has the effect of spreading availability across local fisheries, while the most important effect of the latter is to spread availability throughout the seasons. Both these factors increase the average availability of the recreational resource by accommodating demand that might otherwise saturate atypically productive local fisheries. Finally, the potential value of the national fisheries includes a component determined by (5) the size of the geographical range since the potential value of national fisheries is reduced when all potential salmonid habitat does not support viable local fisheries.

Salmonid fish exploit a diverse set of environments over their species' ranges, using a wide range of life-history strategies that involve marked differences in characters such as size-at-age, age of return and return-timing. Characters like these are manifestly relevant to fishery interests. If any of this variation is genetically based, then genetic variation is a potential determinant of the value of the fishery with regard to factors (2) and (4), above. Additionally, a copious literature demonstrates that structuring of salmonids into distinct geographically or behaviourally distinct reproductive populations (i.e. groups of fish within which mating is random but among which interbreeding is essentially absent) is a prominent feature of the biology of both brown trout and Atlantic salmon (see below). Populations are susceptible to the effects of natural selection and, under many circumstances, local genetic adaptation is expected. If local adaptation is a feature of salmonid populations then genetic diversity will also be a determinant of both abundance and distribution and, therefore of importance for factors (1), (3) and (5), listed above. Genetic effects are therefore potentially an element influencing all five factors related to the value of the fisheries and, potentially, a matter of self-interest for fishery managers.

This paper examines this case in some detail and it has three objectives. The first is to review population structuring in salmon and trout in order to consider the rates at which fish and genes are exchanged between populations and the way in which populations relate to one another. Among salmonid populations, performance varies greatly for a diverse set of characters and the second objective is to assess whether any of these variations are likely to reflect genetic adaptation to local environmental conditions. The third objective is to consider the nature and the extent of the constraints that population structuring and local genetic adaptation may place on management. We consider these objectives in relation to Atlantic salmon and brown trout, in the context of the more general literature that has built up over recent years. Our overall aim is to develop an approach that reconciles society's general requirement for the long-term maintenance of biodiversity with the narrower, more practical requirement of fisheries management to maximise economic value in the shorter term.

## 2. Population structuring

A number of complementary approaches can be used to investigate the extent to which individuals form population groupings. Thus, patterns of mating can be observed directly in behavioural studies of physically tagged individuals and their offspring. The main limitations of behavioural evidence are the practical and resource difficulties involved in tagging and monitoring sufficient fish to provide robust assessments in a sufficient number of locations to derive principles that can be generally applied. In the case of anadromous salmonids, the difficulty of linking parents and their offspring is particularly acute. Alternatively, information on patterns of mating can be inferred from patterns in the distribution of genetic variation. This information can be obtained on extensive scales. Thus, phenotypic variation is commonly observed for a range of traits although the genetic element of these variations is often postulated rather than proven. In contrast, molecular genetic techniques have the particular strength of targeting variation that is explicitly genetic, although their power is limited in practice, because even the most comprehensive studies are based on sampling only a very small part of the genome. All these sources of evidence can be combined to examine whether Atlantic salmon and brown trout are divided into reproductively discrete populations and to consider questions of scale.

### 2.1. Behavioural evidence

Population structuring is a common feature of freshwater fish species exploiting breeding habitats that are often discontinuous or fragmented (de Woody and Avise, 2000). Geographical discontinuities in the distribution of habitat limit the exchange of fish and genes among locations. Under these circumstances, the classical shaping forces of founder effects, bottle-necking and genetic drift are active, especially when the populations affected are small—as is often the case for salmonids. Even when physical barriers between populations are incomplete, exchange between populations is limited by the well-known tendency of salmonids to home to their natal rivers after any pre-reproductive dispersal phase (Saunders, 1967; Stabell, 1984; Dittman and Quinn, 1996; Candy and Beacham, 2000). In some cases, homing can be

shown to be targeted below the catchment level, at natal breeding streams or sites (Youngson et al., 1994; Quinn et al., 1999)—although studies carried out at this spatial level are surprisingly scarce. For Atlantic salmon, a high degree of accurate homing was reported for approximately 50% of adults entering the Girnock Burn in Scotland on the basis of tagging experiments carried out in 1986–1988 (Youngson et al., 1994). This work has continued to the present and the same patterns of return have been observed (unpublished data). Tagging work was extended to another stream in the same river catchment in 1988, and has shown similarly high levels of homing (unpublished data). Unfortunately, straying rates for spawners (defined in terms of successful reproduction) to non-natal areas cannot be determined from the same types of study, and patterns of homing and straying cannot be directly compared. Nevertheless, because many fish home with high precision, salmonids are at least potentially capable of restricting gene flow between breeding locations to the low levels that might foster population differentiation.

### 2.2. Genetic evidence

#### 2.2.1. Atlantic salmon

Examination of a number of classes of genetic marker has elucidated how the homing behaviour of individual Atlantic salmon influences population structure within the species. Early studies on blood proteins (reviewed by Wilkins, 1972) were later augmented by a large number of studies of variation at a limited number of polymorphic allozyme markers (e.g. Ståhl, 1981; Vuorinen, 1982; Ståhl et al., 1983; Cross and Healy, 1993; Ståhl and Hindar, 1988; Koljonen, 1989; Crozier and Moffett, 1989; Verspoor and Cole, 1989; Vuorinen and Berg, 1989; McElligott and Cross, 1991; Blanco et al., 1992; Jordan et al., 1992; Elo, 1993; Galvin et al., 1994; Verspoor, 1994; O'Connell et al., 1995). Collectively, these studies have sampled across the entire species' range.

A hierarchy of genetic differentiation within the species is revealed. At the highest level there are three identified regional groupings: western Atlantic, eastern Atlantic and Baltic (Ståhl, 1987; Verspoor, 1988, 1997). Analysis of mitochondrial DNA (mtDNA) supports the allozyme evidence for the distinctiveness of Atlantic salmon populations in the Baltic from eastern

Atlantic populations (Verspoor et al., 1999). Moreover, within these broad groups, populations from different river systems also show significant genetic differentiation, representing the intermediate level of the genetic hierarchy. At the lowest level, populations within tributaries of major river systems display lower, but still statistically significant genetic divergence (Verspoor et al., 1991; Jordan et al., 1992; Garant et al., 2000). These observations indicate that levels of gene flow (or genetically effective dispersal) between Atlantic salmon populations is low, and lower than would be assumed from observed straying rates (Ståhl, 1981). This apparent discrepancy may arise because estimates of straying are often based on tag returns from fisheries operating some time ahead of spawning and fish may rectify temporary errors in positioning before they reproduce. Alternatively, reproductive fitness may be reduced among fish that have strayed (Tallman and Healy, 1994), or among their progeny. A general lack of correspondence between geographic and genetic distance between populations within the major regional groupings probably reflects the relatively strong influence of genetic drift within populations compared to gene flow between them (Hutchison and Templeton, 1999).

Low levels of polymorphism at allozyme loci in Atlantic salmon (Wilson et al., 1995) stimulated interest in the investigation of DNA markers in an effort to improve the resolution of studies of population structure (Taggart and Ferguson, 1990; Taggart et al., 1995; Galvin et al., 1996) and microsatellite (Sánchez et al., 1996; Fontaine et al., 1997; McConnell et al., 1997; Tessier and Bernatchez, 1999; Tessier et al., 1997; Garant et al., 2000). As expected, both mini- and microsatellite DNA loci have proved to be much more polymorphic than allozyme loci, although patterns of differentiation at DNA loci generally match patterns found previously using allozymes (Sánchez et al., 1996). However, technical advances in molecular biology, and particularly the development of highly polymorphic microsatellite markers, have added new dimensions to studies of Atlantic salmon population structure, particularly at the within-population level (see below). For example, using archived collections of dried scales as a source of DNA, Nielsen et al. (1997, 1999) have established that the pattern of genetic variation among Danish Atlantic salmon populations is temporally stable, even over periods of up to

60 years and despite large scale fluctuations in population size. It is likely that, in future, the use of scale sample collections will yield further important insights into the effects of recent human impact on salmonid populations.

#### 2.2.2. *Brown trout*

The brown trout displays an even more complex and highly differentiated population structure than the Atlantic salmon, probably because of less extensive dispersal in the pre-reproduction phase. Bernatchez and co-workers have identified five major mtDNA lineages across the species' range. Four are named according to the geographic region in which they are most commonly found (Atlantic, Mediterranean, Danubian, Adriatic) and the fifth lineage is for the morphological type, *marmoratus*, the marmorated trout (Bernatchez et al., 1992; Giuffra et al., 1994; Bernatchez and Osinov, 1995; Osinov and Bernatchez, 1996). These lineages are considered to have diverged as a result of isolation due to changes in sea levels and river drainages during recent glaciations. Since the retreat of the glaciers from northern Europe, however, many of the original lineages have come into secondary contact. Multiple lineages are often now present in rivers flowing into the Mediterranean, Black and Caspian Seas, either as introgressed populations or as sympatric populations separated from each other on a microgeographic scale. Most populations of the brown trout in rivers flowing into the Atlantic Ocean, including those for the rivers of the British Isles, appear to be derived from the Atlantic lineage. However, even within these populations there is evidence of at least two waves of post-glacial colonisation (Hamilton et al., 1989; Hynes et al., 1996; García-Marín et al., 1999) with, potentially, some introgression from the Danubian lineage (Osinov and Bernatchez, 1996).

High levels of genetic differentiation among brown trout populations are commonplace on microgeographic scales. As in Atlantic salmon, numerous studies have shown significant allele frequency differences among populations, both between and within rivers (e.g. Allendorf et al., 1976; Ryman et al., 1979; Ferguson and Mason, 1981; Taggart and Ferguson, 1986; Huusko et al., 1990; Stephen and McAndrew, 1990; Skaala, 1992; Hall, 1992; Hansen et al., 1993; Estoup et al., 1998; Hansen and Mensberg, 1998). However, when compared across a similar geographic

range (using  $F_{ST}$  as a statistic to measure population differentiation), brown trout populations display a level of differentiation approximately 10 times greater than that observed in Atlantic salmon (Jordan et al., 1992). Initially, it was suggested that there was no relationship between genetic and geographic distance between brown trout populations on small geographic levels (Crozier and Ferguson, 1986; Stephen and McAndrew, 1990). More recent studies, however, have provided evidence supporting an “isolation by distance” model of gene flow (Estoup et al., 1998; Hansen and Mensberg, 1998; Bouza et al., 1999).

A striking example of the potential complexity of brown trout population structure comes from the relatively small Lough Melvin (21 km<sup>2</sup>) in northwestern Ireland. Here, three forms of brown trout are recognised: so-called ferox, sonaghan and gillaroo. These forms are genetically (Ferguson and Mason, 1981; Ferguson and Fleming, 1983; Ferguson and Taggart, 1991; Prodöhl et al., 1992; McVeigh et al., 1995), morphologically (Cawdery and Ferguson, 1988) and ecologically (Ferguson, 1986) differentiated. They spawn in different tributaries (sonaghan vs. gillaroo) or parts of tributaries (ferox vs. sonaghan), and have distinctly different diets and growth rates. The situation in Lough Melvin, although extreme, does not appear to be unique, even in the British Isles, as morphological, ecological and genetic differentiation of populations has also been observed in Lough Neagh in northern Ireland (Crozier and Ferguson, 1986) and at least two other lakes (McMeel, 1996). A long term study in the English Lake District has demonstrated that two brown trout populations within the same river system differ markedly in many aspects of their ecology (Elliot, 1994), although the basis (genetic or environmental) of the observed differences has not yet been established.

The traditional division of brown trout into anadromous (sea trout) and freshwater-resident (brown trout) components, which are often managed separately, is not well substantiated by work using genetic markers (Hindar et al., 1991; Cross et al., 1992). Although an early study (Skaala and Nævdal, 1989) did suggest that genetic differences existed between resident and anadromous trout in three Norwegian rivers, this has been reinterpreted as microgeographic differentiation (Hindar et al., 1991; Skaala, 1992). Intriguingly, Ferguson et al. (1995) report that although they found

no differences between resident and anadromous fish at nuclear loci (inherited equally through both the paternal and maternal lines), there were significant differences at mitochondrial DNA loci (inherited only through the maternal line). Thus, it may be that female anadromous and resident trout inhabiting the same site represent two “populations”, with gene flow between them mediated by males.

### 2.3. Effects of stock transfers

It can be argued that past management, including the widespread transfer of large numbers of both salmon and trout among locations, is likely to have eroded historical levels of natural population structuring to minimal levels. Transfers of salmonids among locations are known to have been common on both local and extensive scales but many of the records are anecdotal, few offer detailed accounts, and even fewer record the outcome of the transfers. In the latter case, the results of transferring the progeny of Icelandic salmon to the Connecticut River in the eastern USA, for example, indicate that the success of these methods cannot be assured (Orciari and Leonard, 1996). Since historical studies based, for example, on archived scale samples (Nielsen et al., 1997) are still few, the relative extent of past and present structuring cannot be compared. However, the studies reviewed here demonstrate unequivocally that, even now, genetic structuring remains a prominent and fine-grained feature of populations of both salmon and trout across their species' ranges.

## 3. Demographic structuring within populations

During their freshwater phase, salmonid populations exploit catchments that are bounded by impassable physical barriers or by the sea. Within catchments, the patchiness of essential habitats curtails distributions. The dispersal of juveniles after hatch is not extensive (see, e.g. Crisp, 1995), parr hold relatively fixed territories (Halvorsen and Stabell, 1990; Armstrong et al., 1997; Mjølnerod et al., 1999; Juanes et al., 2000) and pre-reproductive homing is to targets set during juvenile life (Dittman and Quinn, 1996). This tendency to spatial stability results in generation-to-generation linkage of genealogical groups within freshwater locations (Carlsson et al.,

1999; Fontaine and Dodson, 1999; Spruell et al., 1999). The numerical size of populations may be measured at any of a number of life stages. However, the size of the spawning group ultimately limits population size and, also, the qualitative attributes of the population. Thus, in the former case, the number of females in the spawning population and their fecundity determine the number of eggs available to be deposited in that location. In the latter case, the residual number of spawners is an effect on the overall genetic variation available to be incorporated at the outset of the next generation, since local abundance ultimately limits effective population size ( $N_e$ ). Low spawning escapement, through low  $N_e$ , decreases the likelihood that genetic variation present previously will be represented in succeeding generations.

Relative spawning success and patterns of mating among individuals are potential additional effects on  $N_e$ . For example, poorly judged mating schemes and enhancement protocols have the effect of lowering  $N_e$  (Ryman and Laikre, 1991; Tessier et al., 1997), while well-designed schemes maintain or increase it (Wang, 1997; Hedrick et al., 2000). Recently, the development of genetic markers has made it possible to investigate internal structuring in natural populations attributable to reproductive behaviour. Individual contributions to spawning can now be documented by following the transmission of hypervariable mini- or microsatellite alleles between the parental generation and the resulting progeny. The few studies available to date are for salmon. They demonstrate that the number of anadromous males is exceeded at spawning by the number of small, non-anadromous males (Thomaz et al., 1997). Treated as a group, small males are capable of obtaining a high proportion of all fertilisations compared with the large males and their activity increases  $N_e$ . During individual spawnings, numerous small males may obtain fertilisations, such that the contents of a single egg pocket constitute multiple, maternal half-sib families. Adult females spawn multiple nests within the same redd, or in multiple redds, often pairing with different sea-run males to do so; adult males are themselves capable of pairing repeatedly, often with different females (Taggart et al., 2001). Multiple pairings of all these types have the effect of increasing the range of possible multi-allele combinations that come to be represented among the progeny group. This effect is potentially important since natural selection acts on

performance traits that are probably most often attributable to the actions of several or many genes acting in concert.

#### 4. Performance variation

Salmonid populations exploit freshwater environments that vary markedly over a wide range of geographical scales. For example, because salmonids are poikilothermic, environmental temperature is a potent determinant of growth and performance. In fresh water, average temperatures, seasonal patterns of variation and extreme values all differ grossly across the geographical ranges of trout and salmon. For anadromous individuals, spatial variations in marine environment have an additional effect on performance, since fish enter the sea from rivers that are widely dispersed around the northern Atlantic seaboard to engage in migrations through the ocean that differ in duration and extent. Given their wide geographical distribution and the disparate habitats they exploit, the performance of salmonids is expected to vary regionally (Friedland, 1998).

More locally, habitat parameters vary grossly between localities within some of the major river catchments. This is due in large measure to the effects of temperature—as it is affected by altitude—on the fish themselves, and on the general ecology of the streams they exploit. As is to be expected, therefore, performance varies between salmonid groups in a large number of observable ways. More particularly, experimental and empirical evidence demonstrates that performance varies on a plausibly genetic basis with respect to a diverse set of qualities evident as differences in the characteristics set out in Table 1.

#### 5. Local adaptation

The performance variations listed above are observed to reside among populations or among other, larger geographical groupings. These variations are therefore candidates for being of locally adaptive significance and the result of natural selection—although, as Adkinson (1995) has cautioned, non-uniform distributions of performance characteristics may also reflect stochastic processes. Direct evidence of local

Table 1

Performance characteristics that are reported to vary among populations or larger geographical groupings of salmonids

Characteristic	Reference
Embryo development	Berg and Moen (1999)
Hatching success	Donaghy and Verspoor (1997)
Juvenile behaviour	Hensleigh and Hendry (1998)
Juvenile performance	McGinnity et al. (1997), Palm and Ryman (1999), Rikardsen and Elliott (2000)
Growth capacity	Conover (1990), Nieceza et al. (1994), McGinnity et al. (1997)
Body morphology	Riddell et al. (1981), Hard et al. (1999)
Habitat preference	Hesthagen et al. (1995)
Timing of smolt migration	Orciari and Leonard (1996)
Migratory behaviour	Jonsson (1982), Svardson and Fagerstrom (1982), Jonsson et al. (1994)
Age at sexual maturity	Hutchings and Jones (1998)
Homing behaviour	Bams (1976), McIsaac and Quinn (1988), Candy and Beacham (2000)
Seasonal run-timing	Saunders (1967), Hansen and Jonsson (1991), Laughton and Smith (1992)
Adult size	Schaffer and Elson (1975), Jonsson et al. (1991)
Timing of spawning	Heggberget (1988), Webb and McLay (1996), Hendry et al. (1999), Sakamoto et al. (1999)
Resistance to the parasite, <i>Gyrodactylus salaris</i>	Bakke et al. (1990), Bakke (1991)

adaptation requires experiments involving reciprocal translocations between sites of individuals from different populations, or raising of individuals from different populations under common environmental conditions. Such experiments are difficult, long-term and expensive for salmonid species (but see McGinnity et al., 1997). Despite the inevitable paucity of direct evidence, there is a wealth of circumstantial evidence for local adaptation in salmonids (reviewed by Taylor, 1991; Elliot, 1994; Verspoor, 1997).

Though natural selection acts on the phenotype, it increases the likelihood that any single genetic variant or (more often) any composite genotype, that confers selective advantage on its holder, will occur in the next generation of the same population. Differential selection reflects the differing survival and reproductive success of various genotypes when exposed to the same environmental constraints. This dynamic tends to increase the fitness of populations through local adaptation if the conditions of selection continue to prevail over succeeding generations. Fixation of populations for a single adaptive variant of any gene is unlikely, since most performance traits are polygenic and since most environments are heterogeneous. It is likely that different gene combinations confer equivalent or near-equivalent average fitness, especially across all the disparate life-cycle phases that precede reproduction in many salmonids. Many different, but superficially equivalent, genetic outcomes can be envisaged

to result. Thus, among individuals within populations, local adaptation need not reflect a single genetic solution and any one of a set of related genotypes may prove to confer approximately similar levels of fitness.

Under some circumstances, however, dichotomous sets of adaptations may result in different ecotypes of the same species exploiting the same environments using disparate life-history strategies with similar levels of success. Thus, genetically separate anadromous and non-anadromous (so-called “land-locked”) populations of Atlantic salmon exist sympatrically in many of the river systems of eastern Canada (Verspoor and Cole, 1989). Other examples occur among the oncorhynchids. Separate genetic populations of summer- and winter-run steelhead (*Oncorhynchus mykiss*) exist in a northern California river (Nielsen and Fountain, 1999). Among sockeye salmon (*O. nerka*), river- and sea-type populations are not highly genetically differentiated. However, they differ markedly from populations of lake-type fish which themselves display high levels of inter-population variation (Gustafson and Winans, 1999).

Currently, most molecular genetic studies of variation among populations are based on markers (i.e. allozyme, mtDNA, minisatellite and microsatellite loci) and the information they generate is generally used with a presumption that the markers are selectively neutral. The study of local adaptation is therefore not obviously amenable to direct investigation by

screening molecular markers. The relationship between levels and patterns of molecular genetic variation and adaptation in performance traits is complex, and to attempt an extrapolation from one to the other may be mistaken and misleading (Hard, 1995). Nevertheless, there does appear to be a general correlation between the level of differentiation at performance traits and neutral molecular markers among populations (Butlin and Tregenza, 1998; Lynch et al., 1999). Furthermore, for the limited number of species for which evidence is available, it seems that between-population differentiation in performance traits is generally greater than that for selectively neutral molecular markers. This suggests that local adaptation of populations is a general phenomenon (Lynch et al., 1999). The presence of outbreeding depression—reduced fitness in progeny of matings between individuals from different populations—also strongly suggests that local adaptation is common (Templeton et al., 1986). However, despite a relationship between individual heterozygosity and some components of fitness (e.g. viability, growth rate, physiological efficiency, fecundity; Mitton, 1993), there is no evidence of a correlation between molecular genetic variation and variation in performance traits within populations (Butlin and Tregenza, 1998; Lynch et al., 1999).

The targeted examination of molecular genetic variation which may have a direct effect on performance traits, and may therefore be influenced by natural selection, is a relatively young but emerging field (Nuzhdin et al., 1999; Purugganan, 2000; Stern, 2000). Genes involved in the immune response, and therefore potentially influencing disease resistance and susceptibility (e.g. those of the major histocompatibility complex, MHC) are of particular interest in salmonids (Hordvik et al., 1993; Grimholt et al., 1993, 2000). In some cases, a single gene of major performance effect has been identified through analysis of loci that were previously assumed to be selectively neutral. In brown trout, kinetic differences observed among allozymes at phosphoglucose isomerase (*PGI-2\** and *PGI-3\**) and lactate dehydrogenase (*LDH-5\**) loci indicate the potential for selective differences among individual genotypes (Henry and Ferguson, 1986, 1987). Indeed, it has been proposed that the increased frequency of the *LDH-5\*90* allele in anadromous brown trout populations of northwest

Europe is due to the action of natural selection (Ferguson and Fleming, 1983; Hamilton et al., 1989). In Atlantic salmon, genetic variation at transferrin (*Tf*; Verspoor, 1986), trypsin (*TRP-2\**; Torrissen, 1991) and a regulatory locus (*PGM-1r\**; Pollard et al., 1994) has been associated with variation in growth rates and life-history type.

Perhaps the best evidence for local adaptation at a single gene in salmonids comes from work on a malic enzyme locus (*MEP-2\**) in Atlantic salmon (Jordan et al., 1997). Allele frequencies in populations in both Europe and North America are significantly correlated with summer freshwater temperatures (Verspoor and Jordan, 1989). The same pattern of correlation between allele frequency and summer water temperature is found among tributaries within major river systems (Verspoor and Jordan, 1989; Verspoor et al., 1991). This pattern of differentiation among populations is likely to arise from temperature-related differences in growth rate (Jordan and Youngson, 1992; Gilbey et al., 1999) and age at first reproduction (Jordan et al., 1990; Morán et al., 1994) that are observed within populations. There is no evidence, as yet, that there are functional differences between *MEP-2\** allozymes. However, the relationships between genotype and the various components of fitness, and observations that extend across the entire species range suggest—at the very least—that *MEP-2\** is tightly linked to another locus, or a group of loci, that strongly influence performance (Jordan et al., 1997).

## 6. Management of populations

Populations of salmon and trout comprise spawning aggregations that are reproductively, and therefore genetically, discrete and within which mating is essentially random. Populations are therefore the smallest, non-divisible biological units that underpin recruitment to the fisheries and they are, therefore, at the core of any genetically based approach to management. In some respects, the properties of populations make it difficult to assimilate population-based concepts into management practice. For example, although salmonid populations are aggregated during spawning and during juvenile life, they are often dispersed and mixed in the pre-reproductive phase during which most fisheries are active. Even before dispersal, the

spatial boundaries of populations cannot be defined with precision. Since fine-scale geographical structuring is commonplace, it also appears highly probable that populations are numerous, and very likely that some populations are small. Usually, limitations in management resources are likely to prevent management initiatives at the finest levels, even if population structure could be sufficiently resolved at these scales.

An expedient approach is needed to address this practical dilemma. One approach might be to cast larger numbers of single genetic populations into smaller numbers of composite groupings where the populations share sufficient relatedness to make them amenable to the same forms of management. This approach is potentially flexible since nested or interchangeable groupings can probably be derived that relate specifically to particular management targets. Thus, for example, groupings that permit the regulation of local marine fisheries operating during the dispersed phase of life may well differ from the groupings appropriate to consideration of the effects of climate change, for example, acting on the same populations during juvenile stream life.

In considering how to make the most appropriate groupings, fisheries managers can usefully borrow from a series of related concepts that have been developed to facilitate the conservation of genetic diversity at the population level. Bowen (1999) has identified three linked themes that are of importance academically and also in the practice of fisheries management—ecology, systematics and evolution. The themes are complementary, although they emphasise different aspects of population structure. The first theme has generated the concept of the Management Unit (Moritz, 1994a) which stresses the ecological context of populations. The concept of the Evolutionary Significant Unit (Moritz, 1994b; Waples, 1995) stresses the systematics theme, and Bowen (1998) has proposed a third concept, the Geminant Evolutionary Unit to accommodate the evolutionary theme. All these conceptual units are based on genetic analysis and have come to relate to the conservation of genetic variations per se, rather than to more general themes in practical management or conservation. However, fisheries management and its two main sub-themes—regulation and enhancement—can usefully borrow from them all. Beyond this, Crandall et al. (2000) have argued for a weakening of the explicitly

genetic nature of conservation units, and a return to the original concepts that also incorporate properties that are plausibly, even if not explicitly, genetic into the pool of information used to define conservation units. Again, fisheries management can borrow from this more pragmatic approach, using general insights to reinforce genetic data, or to replace them when they are not available.

Each of the three genetic management concepts listed above is explicitly unitary, but all can be used to generate groupings broadly based on the metapopulation paradigm. The metapopulation emphasises hierarchical patterns of relatedness among populations. It envisages a spatial array of populations, showing high levels of temporal independence tempered by low levels of contact. Intuitively, the metapopulation appears a potentially powerful construct in a range of management contexts, even though supporting field evidence for the practical application of the theory is presently lacking (Hanski, 1998; Cooper and Mangel, 1999; Young, 1999; Garant et al., 2000; Rieman and Dunham, 2000). Using the metapopulation construct as a template, appropriate ways for combining populations into the larger entities necessary for fisheries management purposes can probably be devised, having full regard to the more general importance of sustaining the ecological, systematics and evolutionary themes.

In defining fisheries-biased management units, managers must aggregate genetic populations into functionally related groupings that co-vary for fishery-related parameters that are biologically meaningful. This must be done in the context of knowledge of underlying population structure based on explicitly genetic insights or, inferentially, on the basis of a general understanding of population genetic concepts. In some cases, covariance in performance may reside only at a geographical level—among contiguous populations within a single river catchment, for example, or within a contiguous group of catchments. As a result, the relevant management units will be defined as relatively simple, spatial aggregation of populations. In other cases, however, more meaningful groupings might be applied based on an additional consideration of performance variation. Thus, for example, the genetically distinct sympatric populations of salmonids cited in the previous section of this text (Verspoor and Cole, 1989; Gustafson and Winans, 1999; Nielsen

and Fountain, 1999) are best treated according to a combination of performance and geographical criteria, rather than by geography alone. Similarly, it is highly likely that populations driving the various seasonal runs of salmon (which distinguish the fisheries of the UK and Ireland from most others) might form the basis of similar, performance-based groupings.

The latter case can be evaluated in the framework developed above. Thus, the productive performance of fisheries based on populations generating early running Atlantic salmon (so-called “spring” salmon and early running grilse) shows a strong tendency to co-vary among river catchments and to vary independently of populations producing other types of fish (unpublished data). Populations generating early running fish show spatial structuring, typically dominating the higher altitude reaches of catchments in which they occur (Laughton and Smith, 1992). The early running habit is heritable (unpublished data) and it is highly likely that it is locally adaptive, although the basis of any adaptation is not known. Populations generating early running fish are distinguished from others by other explicitly genetic factors. Genetic structuring within catchments is common (see above). More specifically, the 125 allele at the *MEP-2\** locus tends to be associated with the relatively colder, higher altitude freshwater environments that early running fish use for spawning (see above). Populations driven by early running fish are therefore characterised by relatively higher frequencies of the 125 allele. In addition, *MEP-2\** genotype is linked with performance variation, both in freshwater and in the sea (see above). Finally, the timing of spawning (a plausibly adaptive performance trait) is earlier for early running fish than for later-running types (Webb and McLay, 1996). Assimilating all this information in a metapopulation framework, suggests that functional relatedness among high altitude locations in contiguous catchments is likely to be greater than among high altitude and low altitude sectors in the same catchment. If so, grouping freshwater populations according to altitude, across catchments, for the enhancement of the early running components of the fisheries appears to be appropriate. Equally, since time of return to rivers is a proxy for eventual spawning location (Laughton and Smith, 1992), it is similarly appropriate to group seasonal elements of the fisheries for the regulation of exploitation.

Both these management approaches identify rational, fisheries-biased groupings that have the particular merit of being consistent with the conservation of the genetic populations on which the fisheries are based.

## 7. Discussion

As reviewed above, an abundance of information based on a wide range of studies indicates that population structuring exists for both salmon and trout throughout their geographical ranges. Evidence of performance variations, plausibly attributed to local adaptation, is compelling enough to suggest that the use of a precautionary approach to management that takes population structuring into account is essential. The thrust of the evidence for structuring and adaptation also establishes the relevance of genetic considerations to the economics of the fisheries, according to the case outlined near the beginning of this paper. Genetic considerations are therefore a matter of self-interest for salmonid fishery management, aside from the more general issue of the value of biodiversity.

From a biodiversity perspective, the exact details of genetic structuring are of undoubted interest. However, for fisheries management, the fine-scale conservation of particular variant alleles, or their frequencies or distributions, for example, will certainly be judged too restrictive a criterion for action. On the other hand, biodiversity considerations link strongly with fisheries management practice, through a strong, shared interest in local genetic adaptation and its conservation. Thus, patterns of local adaptation are of unquestionable interest to all three conservation themes (i.e. genes, species and ecosystems) identified by Bowen (1999) and also to the more practical considerations of fisheries management.

Population structuring is detectable on a range of spatial scales that extends down to sub-catchment levels. One of the extremes in the range of discontinuities can be identified. Thus, in the case of brown trout isolated by waterfalls or living in lakes without patent connection with other bodies of water, inward gene flow is zero. Below this high level of exclusion, examples of isolation-by-distance or “stepping stone” type scenarios of exchange have been identified. Although the nature of inter-population boundary zones remains

unknown, individual salmonids are capable of precise homing at fine geographical scales that are sufficient to limit genetic exchange among populations when spawning takes place. Indeed, it is worth noting that population structuring based on the homing behaviour of individuals has an immediate, ecological relevance that transcends genetic considerations. Homing links the productivity of particular geographical localities across inter-generational time-scales. Thus, any local deficit in spawning will not be immediately or substantially compensated by recruitment of spawners drawn from less depleted spawning populations elsewhere, and stream production of juvenile fish may fall below potential capacity.

As Taylor and Dizon (1999) have pointed out, laboratory genetics is practised with a strong bias towards acceptance of null hypotheses. Consequently, the extent and order of real structuring of genetic variation among salmonids is likely to exceed that which is evident from the literature. Furthermore, functional variation, including adaptive variation, can exist in the absence of parallel variation in the necessarily small sample of allele markers usually deployed in laboratory studies of genetic structuring. In the special context of the fisheries, a precautionary approach to management aims to conserve inter- and intra-population variation in order to maximise the economic value of the resource. From a fisheries management perspective, therefore, the most relevant appreciation of the likely scope for conservation can be gained by using a composite of knowledge (Crandall et al., 2000). The most powerful expedient approach views the morphological, ecological, physiological and behavioural features of populations, against a background knowledge of patterns of explicitly genetic variation.

The concept of population structuring is informative for management and, in view of the strength of the evidence, should now become one of fishery management's canons. The relevant spatial scales for structuring should be recognised and management should be practised according to these. This is already the case in the Pacific North America where the weight of empirical and genetic evidence has been sufficient to establish microevolution and local adaptation as a basis for salmonid management (see, e.g. NRC, 1996). It will likewise be necessary to devise a set of procedures for the management of

Atlantic salmonid fisheries that is consistent with the conservation of population structuring.

However, developing a fully precautionary approach requires that a further issue of importance should be accommodated—namely, the almost certainly dynamic natures of both local adaptation and population structuring (Lande and Shannon, 1996; Bowen, 1998). For salmonids, as for other animals, knowledge is lacking of historical systems of change and the routes that led to population structuring as it is currently observed. More critically, however, no basis exists on which to predict future changes in local selective pressures or to predict future systems of adaptive response (Youngson and Verspoor, 1998). Thus conservation usually assesses population structuring in terms of its current form, and local adaptation is treated as a response to selective pressures that are currently active. The broader approach, however, should also accommodate responses to selective pressures (including, for example, climate change) that vary across time. Accordingly, retention of adaptive genetic capacity within and among salmonid populations must be considered among fisheries management's main aims, and a commitment to conserve a capacity for change must therefore be added to the more conventional commitment to conserve existing structure. This slight paradox can be resolved without difficulty (Bowen, 1998, 1999) and may, in future, present a rationale for devising a more creative approach to genetic management than can be justified on the basis of present knowledge (Youngson and Verspoor, 1998).

Creative types of management involving transfers between populations may become feasible when the inter-relationships among populations, the performance variation they encompass, the extent of local adaptation and the consequences of adaptation for population persistence are much better understood. Now, in the almost total absence of this knowledge, only conservative and precautionary approaches to management can be considered to be valid. No management intervention can be envisaged that is completely free of effects on population structuring and, as an expedient, fisheries management must devise valid ways to offset future biodiversity needs against current fishery requirements. The essence of the problem of reconciling these partly divergent interests can then be seen to concern a balance of techniques and

approaches to management, and a balance in the force with which they are applied.

Incorporating the genetic dimension of salmonid biology into management will require the modification of many current practices. As a default position, management should operate securely within the constraints that population structuring imposes. Injudicious or gratuitous introductions or transfers among populations should not take place and planned actions should attempt to compare the real likely gains in productivity against contingent effects on population structuring. The use of salmon of farmed origin for stocking, for example, has a superficial attraction that can be shown to be illusory. The progeny of farmed stock out-performed and displaced native fish at the juvenile stage but did not return at expected frequencies from the ocean (Einum and Fleming, 1997; McGinnity et al., 1997; Ferguson et al., unpublished data). Enhancement should be based on local brood-stock and mating schemes that are stratified and quasi-natural. When transfer among locations is necessary, matched stocks from similar environments in nearby catchments should be used. Recently, Young (1999) has integrated these concepts formally in the context of the metapopulation paradigm, proposing that introductions can be rationalised in terms of the manipulation of natural straying rates among sites. The nature of populations should continue to be explored using complementary studies based on genetic, and behavioural and performance variations, in order to further facilitate local management.

No fisheries are without effect on salmonid populations since fishing mortality reduces the size of adult spawning populations and limits the range of genetic variation available to be represented in the progeny generation. In some respects, the effect of fishing mortality among female salmonids is likely to have more impact, since a relatively larger part of the maturing females may be susceptible to exploitation because of their tendency to greater age and greater body size. In contrast, only the larger fish among the male spawning group are likely to be exploited and, additionally, any loss of genetic variation due to fishing mortality among large males is likely to be compensated by increased spawning opportunities for small males. On the other hand, the size-selective nature of most fisheries can be seen to militate against the spawning of larger fish generally, on the basis of the expression of

heritable traits for faster growth or for greater size at maturity.

Thus, while fisheries regulation is often carried out on a solely numerical basis, there are qualitative aspects to management that must also be considered. These include ensuring that exploitation is not overly biased towards a particular component of single populations by, for example, size-selective fisheries. Management must also ensure that exploitation falls evenly among numerically robust populations, in order to avoid distortions in inter-population exchange of fish and genes. Relatively greater protection must be afforded to small or failing populations, in order to maintain their productive capacity within the wider grouping, and also in order to conserve their genetic status.

Beyond these considerations, phenotypic and adaptive genetic potential is limited on local geographical scales by the total potential of the species, and also by temporal and spatial rates of exchange at the population level where parts of the total variation reside. In order to conserve adaptive potential it is necessary to conserve high intrinsic levels of variation at all spatial scales and, in particular, to conserve diversity in performance at whatever population level it resides. Within populations, effective population size should be maintained at high levels in order to foster the local retention of potentially adaptive genetic variation. By these means, broad-scale variety and local adaptive potential will be conserved. In addition, local adaptive potential should be enhanced through the maintenance of high levels of abundance in all populations, in order to conserve the dynamic aspects of population structure through the natural exchange of fish and genes among populations. In these ways, fisheries managers can aim to promote the numerical productivity of the fisheries, while giving new weight to the promotion of the adaptive variety that adds so much to their aesthetic and economic value.

## References

- Adkinson, M.D., 1995. Population differentiation in Pacific salmon: local adaptation, genetic drift, or the environment? *Can. J. Fish. Aquat. Sci.* 52, 2762–2777.
- Allendorf, F.W., Ryman, N., Stennek, A., Ståhl, G., 1976. Genetic variation in Scandinavian brown trout (*Salmo trutta* L.): evidence of distinct sympatric populations. *Hereditas* 83, 73–82.

- Armstrong, J.D., Braithwaite, V.A., Huntingford, F.A., 1997. Spatial strategies of wild Atlantic salmon parr—exploration and settlement in unfamiliar areas. *J. Anim. Ecol.* 66, 203–211.
- Bakke, T., 1991. A review of the inter- and intraspecific variability in salmonid hosts to laboratory infections with *Gyrodactylus salaris* Malmberg. *Aquaculture* 98, 303–310.
- Bakke, T.A., Jansen, P.A., Hansen, L.P., 1990. Differences in the host resistance of Atlantic salmon, *Salmo salar* L., stocks to the monogenean *Gyrodactylus salaris* Malmberg, 1957. *J. Fish Biol.* 37, 577–587.
- Bams, R.A., 1976. Survival and propensity for homing as affected by presence or absence of locally adapted paternal genes in two transplanted populations of pink salmon (*Oncorhynchus gorbusha*). *J. Fish. Res. Bd. Can.* 33, 2716–2725.
- Berg, O.K., Moen, V., 1999. Inter- and intra-population variation in temperature sum requirements at hatching in Atlantic salmon. *J. Fish Biol.* 54, 636–647.
- Bernatchez, L., Osinov, A., 1995. Genetic diversity of trout (genus *Salmo*) from its eastern native range based on mitochondrial DNA and nuclear gene variation. *Mol. Ecol.* 4, 285–297.
- Bernatchez, L., Guymard, R., Bonhomme, F., 1992. DNA sequence variation of the mitochondrial control region among geographically and morphologically remote European brown trout, *Salmo trutta*, populations. *Mol. Ecol.* 1, 161–173.
- Blanco, G., Sanchez, J.A., Vazquez, E., Rubio, J., Utter, F.M., 1992. Genetic differentiation among natural European populations of Atlantic salmon, *Salmo salar* L., from drainages of the Atlantic Ocean. *Anim. Genet.* 23, 11–18.
- Bouza, C., Arias, J., Sánchez, C.L., Martínez, P., 1999. Genetic structure of brown trout, *Salmo trutta* L., at the southern limit of the distribution of the anadromous form. *Mol. Ecol.* 8, 1991–2001.
- Bowen, B.W., 1998. What is wrong with ESUs? The gap between evolutionary theory and conservation principles. *J. Shellfish Res.* 17, 1355–1358.
- Bowen, B.W., 1999. Preserving genes, species, or ecosystems? Healing the fractured foundations of conservation policy. *Mol. Ecol.* 8, S5–S10.
- Butlin, R.K., Tregenza, T., 1998. Levels of genetic polymorphism: marker loci versus quantitative traits. *Phil. Trans. R. Soc. Lond. B* 353, 187–198.
- Candy, J.R., Beacham, T.D., 2000. Patterns of homing and straying in southern British Columbia coded-wire tagged chinook (*Oncorhynchus tshawytscha*) populations. *Fish. Res.* 47, 41–56.
- Carlsson, J., Olsen, K.H., Nilsson, J., Overli, O., Stabell, O.B., 1999. Microsatellites reveal fine-scale genetic structuring in stream-living brown trout. *J. Fish Biol.* 55, 1290–1303.
- Cawdery, S.A.H., Ferguson, A., 1988. Origins and differentiation of three sympatric species of trout (*Salmo trutta* L.) in Lough Melvin, Ireland. *Pol. Arch. Hydrobiol.* 35 (Suppl. A), 267–277.
- Conover, D.O., 1990. The relation between capacity for growth and length of growing season: evidence for and implications of countergradient variation. *Trans. Am. Fish. Soc.* 119, 416–430.
- Cooper, A.B., Mangel, M., 1999. The dangers of ignoring metapopulation structure for the conservation of salmonids. *Fish. Bull.* 97, 213–226.
- Crandall, K.A., Bininda-Emonds, O.R.P., Mace, G.M., Wayne, R.K., 2000. Considering evolutionary processes in conservation biology. *Trends Ecol. Evol.* 15, 290–295.
- Crisp, D.T., 1995. Dispersal and growth rate of 0-group salmon (*Salmo salar* L.) from point-stocking together with some information from scatter-stocking. *Ecol. Freshwater Fish* 4, 1–8.
- Cross, T.F., Healy, J.A., 1993. The use of biochemical genetics to distinguish stocks of Atlantic salmon, *Salmo salar* L., in Ireland. *Irish Fish. Invest. Ser. A* 23, 61–66.
- Cross, T.F., Mills, C.P.R., de Courcy Williams, M., 1992. An intensive study of allozyme variation in freshwater resident and anadromous trout, *Salmo trutta* L., in western Ireland. *J. Fish Biol.* 40, 25–32.
- Crozier, W.W., Ferguson, A., 1986. Electrophoretic examination of the population structure of brown trout, *Salmo trutta* L., from the Lough Neagh catchment, Northern Ireland. *J. Fish Biol.* 28, 459–477.
- Crozier, W.W., Moffett, I.J.J., 1989. Amount and distribution of biochemical genetic variation among wild populations and a hatchery stock of Atlantic salmon, *Salmo salar* L., from north-east Ireland. *J. Fish Biol.* 35, 665–677.
- de Woody, J.A., Avise, J.C., 2000. Microsatellite variation in marine, freshwater and anadromous fishes compared with other animals. *J. Fish Biol.* 56, 461–473.
- Dittman, A.H., Quinn, T.P., 1996. Homing in Pacific salmon: mechanisms and ecological basis. *J. Exp. Biol.* 199, 83–91.
- Donaghy, M.D., Verspoor, E., 1997. Egg survival and timing of hatch in two Scottish Atlantic salmon stocks. *J. Fish Biol.* 51, 211–214.
- Einum, S., Fleming, I.A., 1997. Genetic divergence and interactions in the wild among native, farmed and hybrid Atlantic salmon. *J. Fish Biol.* 50, 634–651.
- Elliot, J.M., 1994. *Quantitative Ecology and the Brown Trout*. Oxford University Press, Oxford.
- Elo, K., 1993. Gene flow and conservation of genetic variation in anadromous Atlantic salmon (*Salmo salar*). *Hereditas* 119, 149–159.
- Estoup, A., Rousset, F., Michalakis, Y., Cornuet, J.-M., Adriamanga, M., Guymard, R., 1998. Comparative analysis of microsatellite and allozyme markers: a case study investigating microgeographic differentiation in brown trout (*Salmo trutta*). *Mol. Ecol.* 7, 339–353.
- Ferguson, A., 1986. Lough Melvin—a unique fish community. *Occasional Papers Irish Sci. Technol.* 1, 1–17.
- Ferguson, A., Fleming, C.C., 1983. Evolutionary and taxonomic significance of protein variation in the brown trout (*Salmo trutta* L.) and other salmonid fishes. In: Oxford, G.S., Rollinson, D. (Eds.), *Protein Polymorphism: Adaptive and Taxonomic Significance*. Academic Press, London, pp. 85–99.
- Ferguson, A., Mason, F.M., 1981. Allozyme evidence for reproductively isolated sympatric populations of brown trout (*Salmo trutta* L.) in Lough Melvin, Ireland. *J. Fish Biol.* 18, 629–642.
- Ferguson, A., Taggart, J.B., 1991. Genetic differentiation among the sympatric brown trout (*Salmo trutta*) populations of Lough Melvin, Ireland. *Biol. J. Linn. Soc.* 43, 221–237.
- Ferguson, A., Taggart, J.B., Prodöhl, P.A., McMeel, O., Thompson, C., Stone, C., McGinnity, P., Hynes, R.A., 1995. The application

- of molecular markers to the study and conservation of fish populations, with special reference to the genus *Salmo*. J. Fish Biol. 47 (Suppl. A), 103–126.
- Fontaine, P.-M., Dodson, J.J., 1999. An analysis of the distribution of juvenile Atlantic salmon in nature as a function of relatedness using microsatellites. Mol. Ecol. 8/2, 189–198.
- Fontaine, P.-M., Dodson, J.J., Bernatchez, L., Slettan, A., 1997. A genetic test of metapopulation structure in Atlantic salmon (*Salmo salar*) using microsatellites. Can. J. Fish. Aquat. Sci. 54, 2434–2442.
- Friedland, K.D., 1998. Ocean climate influences on critical Atlantic salmon (*Salmo salar*) life history events. Can. J. Fish. Aquat. Sci. 55 (Suppl. 1), 119–130.
- Galvin, P., Cross, T., Ferguson, A., 1994. Genetic differentiation and gene flow in Atlantic salmon, *Salmo salar* L.: a case study of the River Shannon system in Ireland. Aquacult. Fish. Manage. 25, 131–145.
- Galvin, P., Taggart, J., Ferguson, A., O'Farrell, Cross, T., 1996. Population genetics of Atlantic salmon (*Salmo salar*) in the River Shannon system in Ireland: an appraisal using single locus minisatellite (VNTR) probes. Can. J. Fish. Aquat. Sci. 53, 1933–1942.
- Garant, D., Dodson, J.J., Bernatchez, L., 2000. Ecological determinants and temporal stability of the within-river population structure in Atlantic salmon (*Salmo salar* L.). Mol. Ecol. 9, 615–628.
- García-Marín, J.-L., Utter, F., Pla, C., 1999. Postglacial colonization of brown trout in Europe based on distribution of allozyme variants. Heredity 82, 46–56.
- Gilbey, J., Verspoor, E., Summers, D., 1999. Size and *MEP-2\** variation in juvenile Atlantic salmon (*Salmo salar*) in the River North Esk, Scotland. Aquat. Living Res. 12, 295–299.
- Giuffra, E., Bernatchez, L., Guyomard, R., 1994. Mitochondrial control region and protein coding genes sequence variation among phenotypic forms of brown trout *Salmo trutta* from northern Italy. Mol. Ecol. 3, 161–171.
- Grimholt, U., Hordvik, I., Fosse, V.M., Olsaker, I., Endresen, C., Lie, Ø., 1993. Molecular cloning of major histocompatibility complex class I cDNAs in Atlantic salmon. Immunogenetics 37, 469–473.
- Grimholt, U., Getahun, A., Hermsen, T., Stet, R.J.M., 2000. The major histocompatibility class II alpha chain in salmonid fishes. Dev. Comp. Immun. 24, 751–763.
- Gustafson, R.G., Winans, G.A., 1999. Distribution and population genetic structure of river- and sea-type sockeye salmon in western North America. Ecol. Freshwater Fish 8, 181–193.
- Hall, H.J., 1992. Genetics of Welsh brown trout. Ph.D. Thesis. University of Wales.
- Halvorsen, M., Stabell, O.B., 1990. Homing behaviour of displaced stream-dwelling brown trout. Anim. Behav. 39, 1089–1097.
- Hamilton, K.E., Ferguson, A., Taggart, J.B., Tomasson, T., Walker, A., Fahy, E., 1989. Post-glacial colonisation of brown trout, *Salmo trutta* L.: *Ldh-5* as a phylogeographic marker locus. J. Fish Biol. 35, 651–664.
- Hansen, L.P., Jonsson, B., 1991. Evidence of a genetic component in the seasonal return pattern of Atlantic salmon, *Salmo salar* L. J. Fish Biol. 38, 251–258.
- Hansen, M.M., Mensberg, K.-L.D., 1998. Genetic differentiation and relationship between genetic and geographic distance in Danish sea trout (*Salmo trutta* L.) populations. Heredity 81, 493–504.
- Hansen, M.M., Loeschcke, V., Rasmussen, G., Simonsen, V., 1993. Genetic differentiation among Danish brown trout (*Salmo trutta*) populations. Hereditas 118, 177–185.
- Hanski, I., 1998. Metapopulation dynamics. Nature 396, 41–49.
- Hard, J.J., 1995. A quantitative genetic perspective on the conservation of intraspecific diversity. Am. Fish. Soc. Symp. 17, 304–326.
- Hard, J.J., Winans, G.A., Richardson, J.C., 1999. Phenotypic and genetic architecture of juvenile morphometry in chinook salmon. J. Heredity 90, 597–606.
- Hedrick, P.Q., Hedgecock, D., Hamelberg, S., Croci, S.J., 2000. The impact of supplementation in winter-run chinook salmon on effective population size. J. Heredity 91, 112–116.
- Heggerberget, T., 1988. Timing of spawning in Norwegian Atlantic salmon (*Salmo salar*). Can. J. Fish. Aquat. Sci. 45, 845–849.
- Hendry, A.P., Berg, O.K., Quinn, T.P., 1999. Condition dependence and adaptation-by-time: breeding date, life history, and energy allocation within a population of salmon. Oikos 85, 499–514.
- Henry, T., Ferguson, A., 1986. Kinetic studies on the lactate-dehydrogenase isozymes of the brown trout, *Salmo trutta* L. Comp. Biochem. Physiol. 85B, 491–496.
- Henry, T., Ferguson, A., 1987. Phosphoglucose isomerase isozymes and allozymes of the brown trout, *Salmo trutta* L. Comp. Biochem. Physiol. 88B, 751–756.
- Hensleigh, J.E., Hendry, A.P., 1998. Rheotactic response of fry from beach-spawning populations of sockeye salmon: evolution after selection is relaxed. Can. J. Zool. 76, 2186–2193.
- Hesthagen, T., Hegge, O., Skurdal, J., Dervo, B.K., 1995. Differences in habitat utilization among native, native stocked, and non-native stocked brown trout (*Salmo trutta*) in a hydroelectric reservoir. Can. J. Fish. Aquat. Sci. 52, 2159–2167.
- Hindar, K., Jonsson, B., Ryman, N., Ståhl, G., 1991. Genetic relationships among landlocked, resident, and anadromous Brown Trout, *Salmo trutta* L. Heredity 66, 83–91.
- Hordvik, I., Grimholt, U., Fosse, V.M., Lie, Ø., Endresen, C., 1993. Cloning and sequence analysis of cDNA encoding the MHC class II beta chain in Atlantic salmon (*Salmo salar*). Immunogenetics 37, 437–441.
- Hutchings, J.A., Jones, M.E.B., 1998. Life history variation and growth rate thresholds for maturity in Atlantic salmon, *Salmo salar*. Can. J. Fish. Aquat. Sci. 55 (Suppl. 1), 22–47.
- Hutchison, D.W., Templeton, A.R., 1999. Correlation of pairwise genetic and geographic distance measures: inferring the relative influences of gene flow and genetic drift on the distribution of genetic variability. Evolution 53, 1898–1914.
- Huusko, A., Van Der Meer, O., Koljonen, M.-L., 1990. Life history patterns and genetic differences in brown trout (*Salmo trutta* L.) in the Koutajoki river system. Pol. Arch. Hydrobiol. 37, 63–77.
- Hynes, R.A., Ferguson, A., McCann, M.A., 1996. Variation in mitochondrial DNA and post-glacial colonization of north western Europe by brown trout. J. Fish Biol. 48, 54–67.
- Jonsson, B., 1982. Diadromous and resident trout, *Salmo trutta*: Is their difference due to genetics? Oikos 38, 297–300.

- Jonsson, N., Hansen, L.P., Jonsson, B., 1991. Variation in age, size and repeat spawning of adult Atlantic salmon in relation to river discharge. *J. Anim. Ecol.* 60, 937–947.
- Jonsson, N., Jonsson, B., Skurdal, J., Hansen, L.P., 1994. Differential response to water current in offspring of inlet- and outlet-spawning brown trout, *Salmo trutta*. *J. Fish Biol.* 45, 356–359.
- Jordan, W.C., Youngson, A.F., 1992. The use of genetic marking to assess the reproductive success of mature male Atlantic salmon parr (*Salmo salar* L.) under natural spawning conditions. *J. Fish Biol.* 41, 613–618.
- Jordan, W.C., Youngson, A.F., Webb, J.H., 1990. Genetic variation at the malic enzyme-2 locus and age at maturity in sea-run Atlantic salmon (*Salmo salar*). *Can. J. Fish. Aquat. Sci.* 47, 1672–1677.
- Jordan, W.C., Youngson, A.F., Hay, D.W., Ferguson, A., 1992. Genetic protein variation in natural populations of Atlantic salmon (*Salmo salar*) in Scotland: temporal and spatial variation. *Can. J. Fish. Aquat. Sci.* 49, 1863–1872.
- Jordan, W.C., Verspoor, E., Youngson, A.F., 1997. The effect of selection on estimates of genetic divergence among populations of the Atlantic salmon (*Salmo salar*). *J. Fish Biol.* 51, 546–560.
- Juanes, F., Letcher, B.H., Gries, G., 2000. Ecology of stream fish: insights gained from an individual-based approach to juvenile Atlantic salmon. *Ecol. Freshwater Fish* 9, 65–73.
- Koljonen, M.-L., 1989. Electrophoretically detectable genetic variation in natural and hatchery stocks of Atlantic salmon in Finland. *Hereditas* 110, 23–35.
- Lande, R., Shannon, S., 1996. The role of genetic variation in adaptation and population persistence in a changing environment. *Evolution* 50, 434–437.
- Laughton, R., Smith, G.W., 1992. The relationship between date of river entry and the estimated spawning positions of adult Atlantic salmon (*Salmo salar* L.) in two major Scottish east coast rivers. In: Priede, I.G., Swift, S.M. (Eds.), *Wildlife Telemetry: Remote Monitoring and Tracking of Animals*. Ellis Horwood, Chichester, UK, pp. 423–433.
- Lynch, M., Perender, M., Spitze, K., Lehman, N., Hicks, J., Allen, D., Latta, L., Ottene, M., Bogue, F., Colbourne, J., 1999. The quantitative and molecular genetic architecture of a sub-divided species. *Evolution* 53, 100–110.
- McConnell, S.K.J., Ruzzante, D.E., O'Reilly, P.T., Hamilton, L., Wright, J.M., 1997. Microsatellite loci reveal highly significant differentiation among Atlantic salmon (*Salmo salar* L.) stocks from the east coast of Canada. *Mol. Ecol.* 6, 1075–1089.
- McElligott, E.A., Cross, T.F., 1991. Protein variation in wild Atlantic salmon, with particular reference to southern Ireland. *J. Fish Biol.* 39 (Suppl. A), 35–42.
- McGinnity, P., Stone, C., Taggart, J.B., Cooke, D., Cotter, D., Hynes, R., McCamley, C., Cross, T., Ferguson, A., 1997. Genetic impact of escaped farmed Atlantic salmon (*Salmo salar* L.) on native populations: use of DNA profiling to assess freshwater performance of wild, farmed, and hybrid progeny in a natural river environment. *ICES J. Mar. Sci.* 54, 998–1008.
- McIsaac, D.O., Quinn, T.P., 1988. Evidence for a hereditary component in homing behaviour of chinook salmon (*Oncorhynchus tshawytscha*). *Can. J. Fish. Aquat. Sci.* 45, 2201–2205.
- McMeel, O.M., 1996. Molecular phylogenetics of brown trout (*Salmo trutta* L.) populations. Ph.D. Thesis. The Queen's University of Belfast, Belfast, 214 pp.
- McVeigh, H.P., Hynes, R.A., Ferguson, A., 1995. Mitochondrial DNA differentiation of sympatric populations of brown trout, *Salmo trutta* L., from Lough Melvin, Ireland. *Can. J. Fish. Aquat. Sci.* 52, 1617–1622.
- Mitton, J.B., 1993. Theory and data pertinent to the relationship between heterozygosity and fitness. In: Thornhill, N.W. (Ed.), *The Natural History of Inbreeding and Outbreeding. Theoretical and Empirical Perspectives*. University of Chicago Press, Chicago, pp. 17–41.
- Mjølnerod, I.B., Refseth, U.H., Hindar, H., 1999. Spatial association of genetically similar Atlantic salmon juveniles and sex bias in spatial patterns in a river. *J. Fish Biol.* 55, 1–8.
- Morán, P., Pendás, A.M., García-Vázquez, E., Izquierdo, J.T., Rutherford, D.T., 1994. Electrophoretic assessment of the contribution of transplanted Scottish Atlantic salmon (*Salmo salar*) to the Esva river (northern Spain). *Can. J. Fish. Aquat. Sci.* 51, 248–252.
- Moritz, C., 1994a. Defining 'evolutionary significant units' for conservation. *Trends Ecol. Evol.* 9, 373–375.
- Moritz, C., 1994b. Applications of mitochondrial-DNA analysis in conservation—a critical review. *Mol. Ecol.* 13, 401–411.
- Nicieza, A.G., Reiriz, L., Brana, F., 1994. Variation in digestive performance between geographically disjunct populations of Atlantic salmon: countergradient in passage time and digestion rate. *Oecologia* 99, 243–251.
- Nielsen, J.L., Fountain, M.C., 1999. Microsatellite diversity in sympatric reproductive ecotypes of Pacific steelhead (*Oncorhynchus mykiss*) from the Middle Fork Eel River, California. *Ecol. Freshwater Fish* 8, 159–168.
- Nielsen, E.E., Hansen, M.M., Loeschcke, V., 1997. Analysis of microsatellite DNA from old scale samples of Atlantic salmon, *Salmo salar*: a comparison of genetic composition over 60 years. *Mol. Ecol.* 6, 487–492.
- Nielsen, E.E., Hansen, M.M., Loeschcke, V., 1999. Genetic variation in time and space: microsatellite analysis of extinct and extant populations of Atlantic salmon. *Evolution* 53, 261–268.
- National Research Council (NRC), 1996. *Upstream: Salmon and Society in the Pacific Northwest*. National Academy Press, Washington.
- Nuzhdin, S.V., Dilda, C.L., Mackay, T.F.C., 1999. The genetic architecture of selection response: inferences from fine-scale mapping of bristle number quantitative trait loci in *Drosophila melanogaster*. *Genetics* 153, 1317–1331.
- O'Connell, M., Skibinski, D.O.F., Beardmore, J.A., 1995. Mitochondrial DNA and allozyme variation in Atlantic salmon (*Salmo salar*) populations in Wales. *Can. J. Fish. Aquat. Sci.* 52, 171–178.
- Orciari, R.D., Leonard, G.H., 1996. Length characteristics of smolts and timing of downstream migration among three strains of Atlantic salmon in a southern New England stream. *N. Am. J. Fish. Manage.* 16, 851–860.
- Osinov, A., Bernatchez, L., 1996. Atlantic and Danubean phylogenetic groupings of brown trout (*Salmo trutta* L.)

- complex: genetic divergence, evolution and conservation. *J. Ichthyol.* 36, 762–786.
- Palm, S., Ryman, N., 1999. Genetic basis of phenotypic differences between transplanted stocks of brown trout. *Ecol. Freshwater Fish* 8, 169–180.
- Pollard, S.M., Danzmann, R.G., Claytor, R.R., 1994. Association between the regulatory locus *PGM-1r\** and life-history types of juvenile Atlantic salmon (*Salmo salar*). *Can. J. Fish. Aquat. Sci.* 51, 1322–1329.
- Prodöhl, P.A., Walker, A., Hynes, R., Taggart, J.B., Ferguson, A., 1992. Genetically monomorphic brown trout (*Salmo trutta* L.) populations, as revealed by mitochondrial DNA, multilocus and single-locus minisatellite (VNTR) analyses. *Heredity* 79, 208–213.
- Purugganan, M.D., 2000. The molecular population genetics of regulatory genes. *Mol. Ecol.* 9, 1451–1461.
- Quinn, T.P., Völk, E.C., Hendry, A.P., 1999. Natural otolith microstructure patterns reveal precise homing to natal incubation sites by sockeye salmon (*Oncorhynchus nerka*). *Can. J. Zool.* 77, 766–775.
- Riddell, B.E., Leggett, W.C., Saunders, R.L., 1981. Evidence of adaptive polygenic variation between two populations of Atlantic salmon (*Salmo salar*) native to tributaries of the Southwest Miramichi River, New Brunswick. *Can. J. Fish. Aquat. Sci.* 38, 321–333.
- Rieman, B.E., Dunham, J.B., 2000. Metapopulations and salmonids: a synthesis of life history patterns and empirical observations. *Ecol. Freshwater Fish* 9, 51–64.
- Rikardsen, A.H., Elliott, J.M., 2000. Variations in juvenile growth, energy allocation and life-history strategies of two populations of Arctic charr in North Norway. *J. Fish Biol.* 56, 328–346.
- Ryman, N., Laikre, L., 1991. Effects of supportive breeding on the genetically effective population size. *Conserv. Biol.* 5, 325–329.
- Ryman, N., Allendorf, F.W., Ståhl, G., 1979. Reproductive isolation with little genetic divergence in sympatric populations of brown trout. *Genetics* 92, 247–262.
- Sakamoto, T., Danzmann, R.G., Okamoto, N., Ferguson, M.M., Ihssen, P.E., 1999. Linkage analysis of quantitative trait loci associated with spawning time in rainbow trout (*Oncorhynchus mykiss*). *Aquaculture* 173, 33–43.
- Sánchez, L., Clabby, C., Ramos, D., Blanco, G., Flavin, F., Powell, R., 1996. Protein and microsatellite single locus variability in *Salmo salar* L. (Atlantic salmon). *Heredity* 77, 423–432.
- Saunders, J.W., 1967. Seasonal patterns of return of Atlantic salmon in the Northwest Miramichi River, New Brunswick. *J. Fish. Res. Bd. Can.* 24, 21–32.
- Schaffer, W.M., Elson, P.F., 1975. The adaptive significance of variations in life history among local populations of Atlantic salmon in North America. *Ecology* 56, 577–590.
- Skaala, Ø., 1992. Genetic population structure of Norwegian brown trout. *J. Fish Biol.* 41, 631–646.
- Skaala, Ø., Nævdal, G., 1989. Genetic differentiation between freshwater resident and anadromous brown trout, *Salmo trutta*, within watercourses. *J. Fish Biol.* 34, 597–605.
- Spruell, P., Rieman, B.E., Knudsen, K.L., Utter, F.M., Allendorf, F.W., 1999. Genetic population structure within streams: microsatellite analysis of bull trout populations. *Ecol. Freshwater Fish* 8, 114–121.
- Stabell, O.B., 1984. Homing and olfaction in salmonids: a critical review with special reference to the Atlantic salmon. *Biol. Rev.* 59, 333–388.
- Ståhl, G., 1981. Genetic differentiation among natural populations of Atlantic salmon (*Salmo salar*) in northern Sweden. In: Ryman, N. (Ed.), *Fish Gene Pools*. *Ecol. Bull.*, Stockholm 34, 95–105.
- Ståhl, G., 1987. Genetic population structure of Atlantic salmon. In: Ryman, N., Utter, F. (Eds.), *Population Genetics and Fishery Management* Seattle. University of Washington Press, pp. 121–140.
- Ståhl, G., Hindar, K., 1988. Genetisk struktur hos norsk laks: status og perspektives. Rapport fra Fiskeforskningen No.1. Direktoratet for Naturforvaltning, Trondheim, Norway.
- Ståhl, G., Loudenslager, E.J., Saunders, R.L., Schofield, E.J., 1983. Electrophoretic study on Atlantic salmon populations from the Miramichi River (New Brunswick) System, Canada. *ICES Anadromous and Catadromous Fish Committee C.M.* 1983/M:20.
- Stephen, A.B., McAndrew, B.J., 1990. Distribution of genetic variation in brown trout, *Salmo trutta* L., in Scotland. *Aquacult. Fish. Manage.* 21, 47–66.
- Stern, D.L., 2000. Evolutionary developmental biology and the problem of variation. *Evolution* 54, 1079–1091.
- Svardson, G., Fagerstrom, A., 1982. Adaptive differences in the long-distance migration of some trout (*Salmo trutta* L.) stocks. *Rep. Inst. Freshwater Res., Drottningholm* 60, 51–80.
- Taggart, J.B., Ferguson, A., 1986. Electrophoretic evaluation of a supplemental stocking programme for brown trout (*Salmo trutta* L.). *Aquacult. Fish. Manage.* 17, 155–162.
- Taggart, J.B., Ferguson, A., 1990. Hypervariable minisatellite DNA single locus probes for the Atlantic salmon, *Salmo salar* L. *J. Fish Biol.* 37, 991–993.
- Taggart, J.B., Prodöhl, P.A., Ferguson, A., 1995. Genetic markers for Atlantic salmon (*Salmo salar* L.): single locus inheritance and joint segregation analyses of minisatellite (VNTR) DNA loci. *Anim. Genet.* 26, 13–20.
- Taggart, J.B., McLaren, I.S., Hay, D.W., Webb, J.H., Youngson, A.F., 2001. Spawning success in Atlantic salmon (*Salmo salar* L.): a long-term DNA profiling based study conducted in a natural stream. *Mol. Ecol.* 10, 1047–1060.
- Tallman, R.F., Healy, M.C., 1994. Homing, straying and gene flow among seasonally separated populations of chum salmon (*Oncorhynchus keta*). *Can. J. Fish. Aquat. Sci.* 51, 577–588.
- Taylor, E.B., 1991. A review of local adaptation in Salmonidae, with particular reference to Pacific and Atlantic salmon. *Aquaculture* 98, 185–207.
- Taylor, B.L., Dizon, A.E., 1999. First policy then science: why a management unit based solely on genetic criteria cannot work. *Mol. Ecol.* 8 (Suppl. 1), S11–S16.
- Templeton, A.R., Hemmer, H., Mace, G., Seal, U.S., Shields, W.M., Woodruff, D.S., 1986. Local adaptation, coadaptation, and population boundaries. *Zoo Biol.* 5, 115–125.
- Tessier, N., Bernatchez, L., 1999. Stability of population structure and genetic diversity across generations assessed by microsatellites among sympatric populations of landlocked Atlantic salmon (*Salmo salar*). *Mol. Ecol.* 8, 169–179.

- Tessier, N., Bernatchez, L., Wright, J.M., 1997. Population structure and impact of supportive breeding inferred from mitochondrial and microsatellite DNA analyses in land-locked Atlantic salmon, *Salmo salar* L. Mol. Ecol. 6, 735–750.
- Thomaz, D., Beall, E., Burke, T., 1997. Alternative reproductive tactics in Atlantic salmon: factors affecting mature parr success. Proc. R. Soc. Lond. B 264, 219–226.
- Torrissen, K.R., 1991. Genetic variation in growth rate of Atlantic salmon with different trypsin-like isozyme patterns. Aquaculture 93, 299–312.
- Verspoor, E., 1986. Spatial correlations of transferrin allele frequencies in Atlantic salmon (*Salmo salar*) populations from North America. Can. J. Fish. Aquat. Sci. 43, 1074–1078.
- Verspoor, E., 1988. Identification of stocks in the Atlantic salmon. In: Strouud, R.H. (Ed.), Proceedings of the Symposium on Future Atlantic Salmon Management, Savannah, Georgia. Marine Recreational Fisheries Series, National Coalition for Marine Conservation, pp. 37–46.
- Verspoor, E., 1994. The evolution of genetic divergence at protein coding loci among anadromous and nonanadromous populations of Atlantic salmon, *Salmo salar*. In: Beaumont, A.R. (Ed.), Genetics and Evolution of Aquatic Organisms. Chapman & Hall, London, pp. 52–67.
- Verspoor, E., 1997. Genetic diversity among Atlantic salmon (*Salmo salar* L.). ICES J. Mar. Sci. 54, 965–973.
- Verspoor, E., Cole, L.J., 1989. Genetically distinct sympatric populations of resident and anadromous Atlantic salmon, *Salmo salar*. Can. J. Zool. 67, 1453–1461.
- Verspoor, E., Jordan, W.C., 1989. Genetic variation at the Me-2 locus in the Atlantic salmon within and between rivers: evidence for its selective maintenance. J. Fish Biol. 35 (Suppl. A), 205–213.
- Verspoor, E., Fraser, N.H.C., Youngson, A.F., 1991. Protein polymorphism within a Scottish river: evidence for selection and estimates of gene flow between tributaries. Aquaculture 98, 217–230.
- Verspoor, E., McCarthy, E.M., Knox, D., Bourke, E.A., Cross, T.F., 1999. The phylogeography of European Atlantic salmon (*Salmo salar* L.) based on RFLP analysis of the ND1/16sRNA region of the mtDNA. Biol. J. Linn. Soc. 68, 129–146.
- Vuorinen, J., 1982. Little genetic variation in the Finnish Lake salmon, *Salmo salar sebago* (Girard). Hereditas 97, 189–192.
- Vuorinen, J., Berg, O.K., 1989. Genetic divergence of anadromous and nonanadromous Atlantic salmon (*Salmo salar*) in the River Namsen, Norway. Can. J. Fish. Aquat. Sci. 46, 406–409.
- Wang, J., 1997. More efficient breeding systems for controlling inbreeding and effective population size in animal populations. Heredity 79, 591–599.
- Waples, R.S., 1995. Evolutionary significant units and the conservation of biological diversity under the Endangered Species Act. In: Nielsen, J.L. (Ed.), Evolution and the Aquatic Ecosystem: Defining Unique Units in Population Conservation. American Fisheries Society Symposium, vol. 17. American Fisheries Society, Bethesda, MD, pp. 8–27.
- Webb, J.H., McLay, H.A., 1996. Variation in the time of spawning of Atlantic salmon (*Salmo salar*) and its relationship to temperature in the Aberdeenshire Dee, Scotland. Can. J. Fish. Aquat. Sci. 53, 2739–2744.
- Wilkins, N.P., 1972. Biochemical genetics of the Atlantic salmon, *Salmo salar* L. I. A review of recent studies. J. Fish Biol. 4, 487–504.
- Wilson, I.F., Bourke, E.A., Cross, T.F., 1995. Genetic variation at traditional and novel allozyme loci, applied to interactions between wild and reared *Salmo salar* L. (Atlantic salmon). Heredity 75, 578–588.
- Young, K.A., 1999. Managing the decline of Pacific salmon: metapopulation theory and artificial recolonization as ecological mitigation. Can. J. Fish. Aquat. Sci. 56, 1700–1706.
- Youngson, A.F., Verspoor, E., 1998. Interactions between wild and introduced Atlantic salmon (*Salmo salar*). Can. J. Fish. Aquat. Sci. 55, 153–160.
- Youngson, A.F., Jordan, W.C., Hay, D.W., 1994. Homing of Atlantic salmon (*Salmo salar* L.) to a tributary stream in a major river catchment. Aquaculture 121, 259–267.