

## **Conservation of genetic variation in harvested salmon populations**

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Management of the sub-structured salmonid species may benefit by considering the genetic structure of the species. In the Atlantic salmon (*Salmo salar*), genetic studies show that populations are genetically distinct, but also that they do not exist in isolation. In this paper, we look at genetic management in a group of populations that are harvested together in the ocean, and separately in fresh water. The scientific problem can be formulated as to combine goals of optimal harvesting and effective population size in a group of populations interconnected by migration. By developing a model that maximises harvesting yield of a group of populations, subject to constraints set by maintaining the total effective size, Tufto & Hindar (2003, *J. Theor. Biol.* 222:273-81) showed that: (1) Considerable gain can be made in total effective size in a group of populations through harvesting based on knowledge about genetic structure, (2) in source-sink population systems, the total effective size can be increased without reducing total yield by first reducing the harvest in the smallest (sink) populations, (3) when populations differ in their degree of isolation, it pays to harvest relatively less in isolated populations, and (4) in cases with directionality in the migration pattern, the total effective size can become less than the sum of the subpopulation sizes. We apply the model to a set of ten salmon populations in western Norway, which is dominated numerically by the River Lærdalselva population. We show that the total effective size of this population system is to a large extent dependent on the effective size of the Lærdalselva population. On the other hand, the smaller populations contribute more to the total *per fish*, than what the Lærdalselva population does. We discuss the results in light of conservation genetic theory and empirical results on the fitness consequences of loss of genetic variation in salmonids, and conclude that the genetic consequences of harvesting need to be assessed both at the level of local (sub)populations and at the level of the total population.

## Introduction

Principles for conservation of genetic variation in natural populations have been related to the population's *effective size*, which is defined as *the size of an ideal population that is losing genetic variation at the same rate as the actual population* (Wright 1969). The effective population size determines the rate of inbreeding of the population and also the rate of loss of heterozygosity and of genetic variance in quantitative traits, such as body size, fecundity, survival, and ultimately, fitness. Empirical evidence from laboratory and domestic animals suggests that increased inbreeding and loss of genetic variation can have negative consequences for a number of fitness-related traits. Moreover, loss of genetic variation can reduce the possibility for a population to adapt to changing environments (Lande & Shannon 1996). For short-term conservation, it has been suggested to maintain effective population sizes above 50 per generation, motivated by the need to keep the rate of inbreeding as low as to avoid inbreeding depression (Frankel & Soulé 1981). For long-term conservation, it has been suggested to maintain effective population sizes above 500 to 5000 in order to preserve typical levels of genetic variability in quantitative characters (Lynch & Lande 1998).

Effective population size has been used as one criterion for determining the extinction risk and setting conservation limits (CLs) of single populations (and/or species), e.g. in international (IUCN) guidelines for categorising threatened species (Mace & Lande 1991). In a fishery management perspective, this translates into finding conservation limits that set constraints on the maximum yield that can be sustainably harvested from the populations. A major weakness, however, is that neither conservation nor optimal harvest criteria are well developed for groups of populations interconnected by gene flow and living in different environments. Such a group of populations is what population geneticists refer to as a 'subdivided population' (Wright 1969), and what many ecologists have termed a 'metapopulation'.

Genetic studies show that Atlantic salmon (*Salmo salar*) from the North American and European continents are highly divergent, with evidence of extremely small or no current gene flow between continents. Within continents, estimates of gene flow between rivers suggest that salmon populations are sufficiently isolated to allow the development of local adaptations through natural selection. The same conclusion may hold for variation between populations belonging to different tributaries of larger river systems. In concordance with this, ecological studies suggest differences among salmon populations in a number of traits that may be important for fitness. Combined, these findings suggest that fitness and productivity may be compromised, if important genetic units of Atlantic salmon are not recognised (Ståhl 1987; Taylor 1991; Verspoor 1997).

The objective of the present paper is to look at how genetic variation is lost from a group of Atlantic salmon populations that are harvested together in one part of the life cycle (the ocean), but may be managed separately in another part of the life cycle (fresh water). We first review some of the evidence for negative fitness consequences of loss of genetic variation. Second, we apply a model for combining effective population size and optimal harvest in a subdivided population (Tufto & Hindar 2003) to a set of Atlantic salmon populations in Norway. Finally, we discuss our findings in a fishery management perspective.

## Fitness consequences of loss of genetic variation

A large body of literature exists from laboratory and domestic animals that show inbreeding depression to follow increased rates of inbreeding in outbreeding species (Frankel & Soulé 1981). Fitness-related traits such as individual growth rate, survival, and fecundity may be negatively affected at 5-10% inbreeding in laboratory populations. Moreover, most inbred lines of laboratory animals go extinct (Frankham 1998). In mice and fruit flies, a threshold effect has been noted for extinction rates, which are moderate for low rates of inbreeding but increase markedly at higher rates of inbreeding (Frankham 1995).

**Table 1** presents some case studies showing fitness consequences of increased inbreeding and/or reduced genetic variation in fish populations. A recent review of inbreeding in salmonids suggests that a 10% increase in inbreeding results in a reduction in fitness from about 3-15% under rapid inbreeding to 1-5% under slow inbreeding (Wang et al. 2002a). It has proven difficult to study the consequences of inbreeding and loss of genetic variation in the wild. For example, Wang et al. (2002a) found only one study of inbreeding depression in salmonids that was carried out in a near-natural situation. In this study, Ryman (1970) showed inbred Atlantic salmon to be recaptured at a lower rate than outbred individuals after release into Swedish streams.

**Table 1.** Empirical observations on negative effects of inbreeding and loss of genetic variation in fishes.

| Species   | Observation  | Reference  |
|---|--|--|
| Atlantic salmon<br><i>Salmo salar</i>                 | Lower survival probability of inbred fish as compared to non-inbred after release into the wild.   | Ryman (1970)   |
| Chinook salmon<br><i>Onchorhynchus tshawytscha</i>    | Homozygotes in one Major Histocompatibility Complex gene have lower survival when exposed to infectious hematopoietic necrosis virus than heterozygotes.<br>Inbred fish have lower resistance to <i>Myxobolus cerebralis</i> (causing whirling disease) than outbred fish. | Arkush et al. (2002)                                 |
|   | Inbreeding (general genomic) and overdominance (local genomic) effects on four reproductive traits.  | Heath et al. (2002)                                  |
| Bullhead <i>Cottus gobio</i>                          | Condition factor positively correlated with genetic diversity in Flemish populations.  | Knaepkens et al. (2002)                              |
| Guppy <i>Poecilia reticulata</i>                      | Salinity tolerance positively correlated with heterozygosity in 17 populations.<br>8.4% decrease in mean salinity tolerance per 10% increase in inbreeding.  | Shikano & Taniguchi (2002);<br>Shikano et al. (2001) |
| Sonoran topminnow<br><i>Poeciliopsis occidentalis</i> | Higher mortality, slower growth rate, lower fecundity, and weaker developmental stability in a homozygous population as compared to more genetically variable populations.   | Quattro & Vrijenhoek (1989)                          |

If homing was perfect, anadromous populations would be perfectly isolated from one another, and a clear relationship between population size and level of neutral genetic variation should be expected. For small populations, we would expect to see very little genetic variation after some generations, and none at all during the time elapsed since the last deglaciation. This is,

however, not the case. Presumably, the gene flow occurring among local populations, even if limited, is sufficient to counteract local variation in overall variability of neutral genes.

In allozyme studies of Atlantic salmon, a low level of genetic variation (heterozygosity) has most often been associated with hatchery stocks and with landlocked populations (Ståhl 1987). A recent study of microsatellite variation in Atlantic salmon by Koljonen et al. (2002) found the highest level of variation in the River Teno/Tana population (both wild and hatchery), which is currently among the biggest salmon populations worldwide. However, nearly as high heterozygosities were found in hatchery stocks from smaller anadromous populations, and only a landlocked population showed a much lower heterozygosity than the Teno. In two comparisons between wild and hatchery stock of the same population, the average rate of loss of heterozygosity in the hatchery derivative was 1.4% per generation and the average observed loss of alleles was 4.7% per generation. The latter observation is consistent with the number of alleles being more sensitive to a reduction in population size than heterozygosity (Ryman et al. 1995).

The relationship between genetic variation and fitness in salmonid fishes seems to vary both among and within species (Wang et al. 2002b). Such a relationship can be affected by genetic background, environment and age, and Wang et al. (2002b) suggest that a necessary tool for conservation issues is to establish relationships between molecular genetic variation, quantitative genetic variation, and phenotypic variation. Although such comparisons are tedious to carry out, they can be established for Atlantic salmon populations that have been extensively analysed by molecular genetic, quantitative genetic and phenotypic methods. A recent example is provided by Koskinen et al. (2002) on European grayling. They conclude that natural selection is the dominant diversifying agent in the life-history evolution of small populations, even though these populations have had small effective population sizes during the 100 years following their release into pristine mountain lakes.

## **Harvesting and effective population size**

How much genetic variation is lost when salmon are caught in coastal fisheries that indiscriminately harvest a number of populations differing in their productivity and genetic constitution?

The scientific problem can be formulated as to combine goals of optimal harvesting (maximum sustainable yield) and effective population size in a group of populations interconnected by migration. This problem was addressed by Tufto & Hindar (2003), who developed a model with constant local population sizes and a fixed but arbitrary pattern of migration, for which the total effective population size can be computed using numerical methods. Next, this model was combined with a simple, deterministic population dynamic model that expresses the rate at which the population is harvested as a function of local population sizes, and emigration and immigration in each subpopulation. Finally, the harvesting yield was maximised subject to constraints set by the effective population size of the total population (Tufto & Hindar 2003). Some results are summarised here:

### ***Effective size of interconnected subpopulations***

- The effective population size in a set of interconnected subpopulations depend on both the rate and pattern of gene flow. Low, symmetric migration rates between subpopulations increase the total effective size (relative to the subpopulation sizes).

- Asymmetric migration, on the other hand, decreases the total effective size. In the extreme case, that is, one-way migration, the total effective size eventually becomes equal to the effective size of the subpopulation emitting migrants (Tufto & Hindar 2003).

#### ***Maximum sustainable yield (MSY) in a set of interconnected subpopulations***

- With deterministic population dynamics and full knowledge of each subpopulation, the effect of migration can be ignored and the optimal harvesting strategy is to harvest each subpopulation to half of its carrying capacity (Tufto & Hindar 2003), which is equal to the 'conservation limit' in NASCO's terminology.

#### ***Maximisation of harvesting yield subject to constraints set by maintaining effective size***

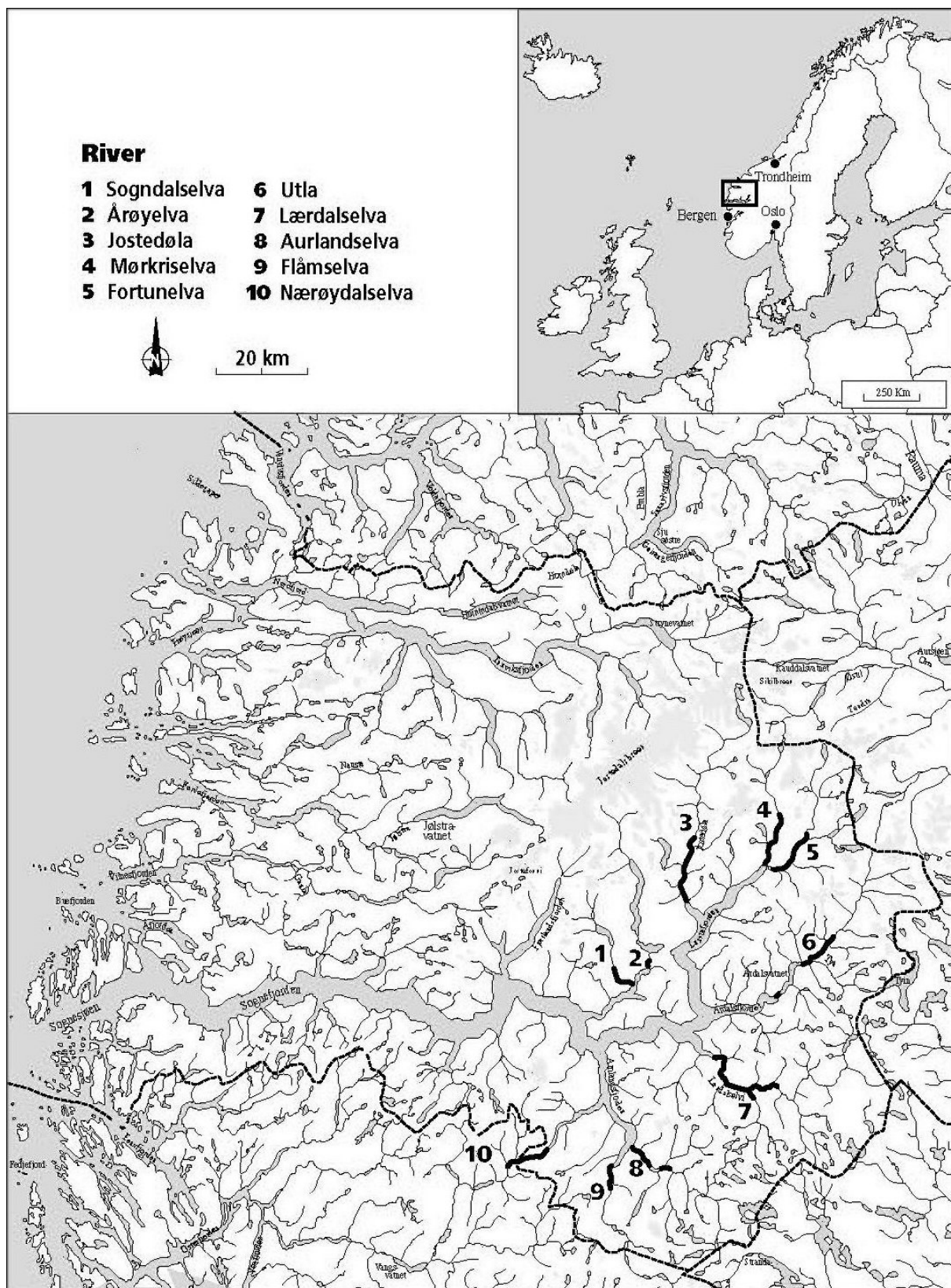
- Considerable gain can be made in total effective size in a group of populations through harvesting based on knowledge about underlying population structure.
- In source-sink population systems (Pulliam 1988), the total effective size can be increased without reducing total harvesting yield by first reducing the harvest in the smallest (sink) population(s), while keeping the harvest in the largest (source) population.
- More can be gained by local adjustment of harvesting when migration rates are low, than when they are high.
- When populations differ in their degree of isolation, it pays off to harvest relatively less in isolated populations because these contribute more to the total effective size (Tufto & Hindar 2003).

### **Application to Atlantic salmon populations**

The above model can be used to compute the effective population size of a subdivided population with constant subpopulation sizes and a fixed but arbitrary pattern of migration among subpopulations. Such data are usually not known for Atlantic salmon populations, but a few cases exist where rough estimates of the number of spawners are available for a set of neighbouring populations, and where some populations have also been subject to tagging studies.

In the Sognefjorden, a 200 km long fjord in western Norway (**Figure 1**), some rivers become so clear during autumn as to allow estimation of the number of spawners present based on counting from the river banks and while diving. The River Lærdalselva (river no. 7) is the most renowned of these rivers, and by far the biggest in terms of production. In the years 1985-1994, on average 459 multi-sea-winter salmon were counted in the autumn before spawning in River Lærdalselva (Sættem 1995). To this, we must add one-sea-winter fish (Vasshaug & Løkensgard 1987), to reach a rough estimate of 540 anadromous spawners annually.

Counts in six other rivers in the same fjord (Sættem 1995) and estimates based on rod catches in three additional rivers, suggest that these rivers have between 10 and 60 anadromous spawners each (**Table 2**). The nine rivers (river nos 1. Sogndalselva, 2. Årøyelva, 3. Jostedøla, 4. Mørkriselva, 5. Fortunelva, 6. Utla, 8. Aurlandselva, 9. Flåmselva and 10. Nærøydalselva) altogether have ca. 310 anadromous spawners. Thus, the total system including the Lærdalselva has around 850 spawners annually. Count estimates of the proportion of the River Lærdalselva population in the total system ( $540/850 = 64\%$ ) is quite similar to one based on marking in the outer part of the fjord of returning adults, 63% of which were recaptured in the Lærdalselva (Vasshaug 1979).



**Figure 1** Map of the Sognefjorden district in western Norway with 10 numbered rivers in the inner part of the fjord. Bold lines show accessible habitat for anadromous Atlantic salmon.

**Table 2.** Estimates of population parameters for Atlantic salmon in 10 rivers in the Sognefjorden district, western Norway. (a) Population sizes from average counts of anadromous spawners per spawning season, (b) forward migration rates from tagging studies of River Lærdalselva salmon, and (c) backward migration rates from combining information in (a) and (b).

(a) Local population sizes

| River no. | N   | River name    |
|-----------|-----|---------------|
| 1         | 60  | Sogndalselva  |
| 2         | 40  | Årøyelva      |
| 3         | 10  | Jostedøla     |
| 4         | 30  | Mørkriselva   |
| 5         | 10  | Fortunelva    |
| 6         | 15  | Utlå          |
| 7         | 540 | Lærdalselva   |
| 8         | 35  | Aurlandselva  |
| 9         | 50  | Flåmselva     |
| 10        | 60  | Nærøydalselva |

(b) Forward migration rates, i.e.  $\tilde{m}_{ij}$  in the matrix is the probability that an individual migrates to subpopulation  $i$  conditional on that it originated from subpopulation  $j$ . The diagonal representing the proportion of homing fish, is highlighted, of which the River Lærdalselva entry has been estimated from tagging.

|       | [,1]         | [,2]         | [,3]       | [,4]         | [,5]       | [,6]         | [,7]         | [,8]         | [,9]        | [,10]        |
|-------|--------------|--------------|------------|--------------|------------|--------------|--------------|--------------|-------------|--------------|
| [1,]  | <b>0.833</b> | 0.050        | 0.0        | 0.000        | 0.0        | 0.000        | 0.015        | 0.000        | 0.02        | 0.067        |
| [2,]  | 0.067        | <b>0.875</b> | 0.0        | 0.000        | 0.0        | 0.000        | 0.007        | 0.000        | 0.00        | 0.033        |
| [3,]  | 0.000        | 0.000        | <b>0.5</b> | 0.033        | 0.1        | 0.000        | 0.007        | 0.000        | 0.00        | 0.000        |
| [4,]  | 0.000        | 0.000        | 0.1        | <b>0.600</b> | 0.3        | 0.000        | 0.019        | 0.000        | 0.00        | 0.017        |
| [5,]  | 0.000        | 0.000        | 0.0        | 0.100        | <b>0.4</b> | 0.000        | 0.007        | 0.029        | 0.00        | 0.000        |
| [6,]  | 0.000        | 0.000        | 0.0        | 0.033        | 0.1        | <b>0.667</b> | 0.007        | 0.000        | 0.00        | 0.017        |
| [7,]  | 0.033        | 0.050        | 0.4        | 0.200        | 0.1        | 0.267        | <b>0.881</b> | 0.114        | 0.08        | 0.083        |
| [8,]  | 0.017        | 0.000        | 0.0        | 0.000        | 0.0        | 0.000        | 0.013        | <b>0.714</b> | 0.08        | 0.017        |
| [9,]  | 0.000        | 0.025        | 0.0        | 0.000        | 0.0        | 0.000        | 0.015        | 0.114        | <b>0.78</b> | 0.050        |
| [10,] | 0.050        | 0.000        | 0.0        | 0.033        | 0.0        | 0.067        | 0.028        | 0.029        | 0.04        | <b>0.717</b> |

(c) Backward migration rates, i.e.  $m_{ij}$  in the matrix is the probability that an individual originated from subpopulation  $j$  conditional on that it migrated to subpopulation  $i$ . Entries for the rivers Lærdalselva and Aurlandselva are highlighted (see text).

|       | [,1]  | [,2]  | [,3]  | [,4]  | [,5]  | [,6]  | [,7]         | [,8]         | [,9]  | [,10] |
|-------|-------|-------|-------|-------|-------|-------|--------------|--------------|-------|-------|
| [1,]  | 0.769 | 0.031 | 0.000 | 0.000 | 0.000 | 0.000 | 0.123        | 0.000        | 0.015 | 0.062 |
| [2,]  | 0.089 | 0.778 | 0.000 | 0.000 | 0.000 | 0.000 | 0.089        | 0.000        | 0.000 | 0.044 |
| [3,]  | 0.000 | 0.000 | 0.455 | 0.091 | 0.091 | 0.000 | 0.364        | 0.000        | 0.000 | 0.000 |
| [4,]  | 0.000 | 0.000 | 0.030 | 0.545 | 0.091 | 0.000 | 0.303        | 0.000        | 0.000 | 0.030 |
| [5,]  | 0.000 | 0.000 | 0.000 | 0.250 | 0.333 | 0.000 | 0.333        | 0.083        | 0.000 | 0.000 |
| [6,]  | 0.000 | 0.000 | 0.000 | 0.059 | 0.059 | 0.588 | 0.235        | 0.000        | 0.000 | 0.059 |
| [7,]  | 0.004 | 0.004 | 0.008 | 0.012 | 0.002 | 0.008 | <b>0.937</b> | <b>0.008</b> | 0.008 | 0.010 |
| [8,]  | 0.026 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | <b>0.184</b> | <b>0.658</b> | 0.105 | 0.026 |
| [9,]  | 0.000 | 0.018 | 0.000 | 0.000 | 0.000 | 0.000 | 0.145        | 0.073        | 0.709 | 0.055 |
| [10,] | 0.045 | 0.000 | 0.000 | 0.015 | 0.000 | 0.015 | 0.227        | 0.015        | 0.030 | 0.652 |

Tagging experiments between 1949 and the 1970s suggest that 4 out of 34 (11.8%) of salmon from the Lærdalselva were recaptured in other rivers (Rosseland 1979; Lars Petter Hansen, NINA, pers. comm.). We have used this estimate as the forward migration rate from the Lærdalselva, and "distributed" the migrants on the other rivers in the Sognefjorden. The migrants make up a significant proportion of spawners in the other rivers (i.e. migration rates in some of the other rivers are up to or more than 50%, **Table 2**). We further assume that this system of one big and several small populations is a source-sink system, such that the nine other rivers combined (the sink) produce fewer migrants to the River Lærdalselva than what the Lærdalselva (the source) contributes to the other nine rivers. To be precise, we assume that 64 strays are produced from the River Lærdalselva population to enter the other nine rivers, which combined produce a total of 32 strays (20 of which are assumed to enter the Lærdalselva).

### ***Relationship between census and effective size***

The effective population sizes of Atlantic salmon populations have not been estimated, but some methods exist to find rough estimates of the effective size or of the ratio of effective to census size. If we look at a single spawning, the effective size is usually much less than the number of breeders. Effective size refers to an ideal population that has discrete generations (all adults reproduce once and at the same age), an equal sex ratio, and the same expected number of offspring per parent. In wild salmon populations, deviation from a 1:1 sex ratio is common among spawners, and a highly skewed reproductive success is the norm rather than the exception (Jones & Hutchings 2002). Another complication is overlapping generations and repeat spawning (iteroparity).

For species that spawn only once (semelparous), a rough estimate of the effective size with overlapping generations, is  $N_e = \tau N_b$ , where  $\tau$  is generation time and  $N_b$  is the effective size per breeding season. A review of estimates from many species suggests that the effective size is often as low as 10-20% of the census size per breeding (Frankham 1995); some experiments with salmonids suggest that the figure may be close to 20%. The generation time for species that spawn only once, is approximately the same as the mean age of the spawners: 5 years would be a reasonable estimate for many salmon populations. Thus, with  $\tau = 5$  and  $N_b/N_{\text{census}} = 0.2$  and ignoring repeat spawning, we suggest as a rule-of-thumb that the effective size of a salmon population per generation ( $N_e$ ) is roughly the same as the census size per breeding season ( $N_{\text{census}}$ ), or  $N_e/N_{\text{census}} \sim 1$ .

Some recent studies of demographic and/or genetic data from salmonid fishes, suggest that  $N_e/N_{\text{census}} = 0.5 - 1.0$  for bull trout, *Salvelinus confluentus* (Rieman & Allendorf 2001),  $N_e/N_{\text{census}} = 0.1 - 0.3$  for steelhead trout, *Oncorhynchus mykiss* (Heath et al. 2002), and  $N_e/N_{\text{census}} = 0.5 - 0.6$  for a population of chinook salmon, *O. tshawytscha* (from Waples 2002). Combined, these studies indicate that our rule-of-thumb represents a slight overestimate of  $N_e$ .

### ***Genetically-based estimate of migration rate***

The number of tagged fish straying from one population to another is not necessarily a good estimate of the number of genetically effective migrants between them. For example, fish that are recorded as strays to another river during the angling season, often several months prior to spawning, have the possibility to "backtrack" before spawning, that is, leave the wrong river and enter the river in which they were born. Moreover, fish that spawn as strays in a non-native river may experience reduced reproductive success if they are less well adapted to local

conditions than homing fish. Finally, migration rates in the equations above usually refer to long-term averages and equilibrium conditions, and not to a single season of migration.

It is possible to estimate genetically effective migration rates from differences in allele frequencies between populations. For an island model of migration (Wright 1969), the standardised variance in allele frequencies at the equilibrium between genetic drift and migration,  $F_{ST}$ , can be related to the genetic effective number of migrants  $N_e m$  by

$$F_{ST} = 1/(4 N_e m + 1).$$

For two of the 10 populations in the Sognefjorden (River Lærdalselva [7] and River Aurlandselva [8]), a preliminary allozyme analysis suggests that  $F_{ST} = 0.032$  and from this,  $N_e m = 7.5$  genetically effective migrants per generation (K. Hindar & T. Balstad, NINA, unpublished). In the table of backward migration rates in the Sognefjorden,  $m_{ij}$  among these populations have been estimated at 0.184 and 0.008, respectively (cf. the highlighted entries in **Table 2c**). If we apply the relationship  $N_e/N_{census} \sim 1$ , then  $N_e$  for the two rivers is  $N_7 = 540$  and  $N_8 = 35$ , respectively (**Table 2a**). This leads to estimates of  $m_{78} = 7.5/540 = 0.014$  and  $m_{87} = 7.5/35 = 0.214$ , respectively. These estimates are not far from the estimates based on the backward migration matrix in **Table 2c**.

#### ***Total effective size for ten neighbouring populations in the Sogn district***

Based on the model by Tufto & Hindar (2003), we have calculated the total effective size of the system of 10 rivers in the Sognefjorden by using estimates of local effective population size from counts and by constructing a migration matrix from a limited set of tagging studies (**Table 2**).

***Effect of source population.*** We first predict the genetic consequences for the whole source-sink system of reducing the population size of the source, the River Lærdalselva, from 540 spawners to zero. This scenario is motivated by the fact that the salmon parasite *Gyrodactylus salaris* has been observed in the River Lærdalselva, and that a dramatic reduction in the population size of this river must be expected. The modelling tool developed by Tufto & Hindar (2003) can be used to calculate total effective size of the system of the ten rivers, as a function of the local effective size in the River Lærdalselva. In terms of exploitation, this scenario would correspond to locally overharvesting the River Lærdalselva population to extinction, for example by a 100% effective trap on this river.

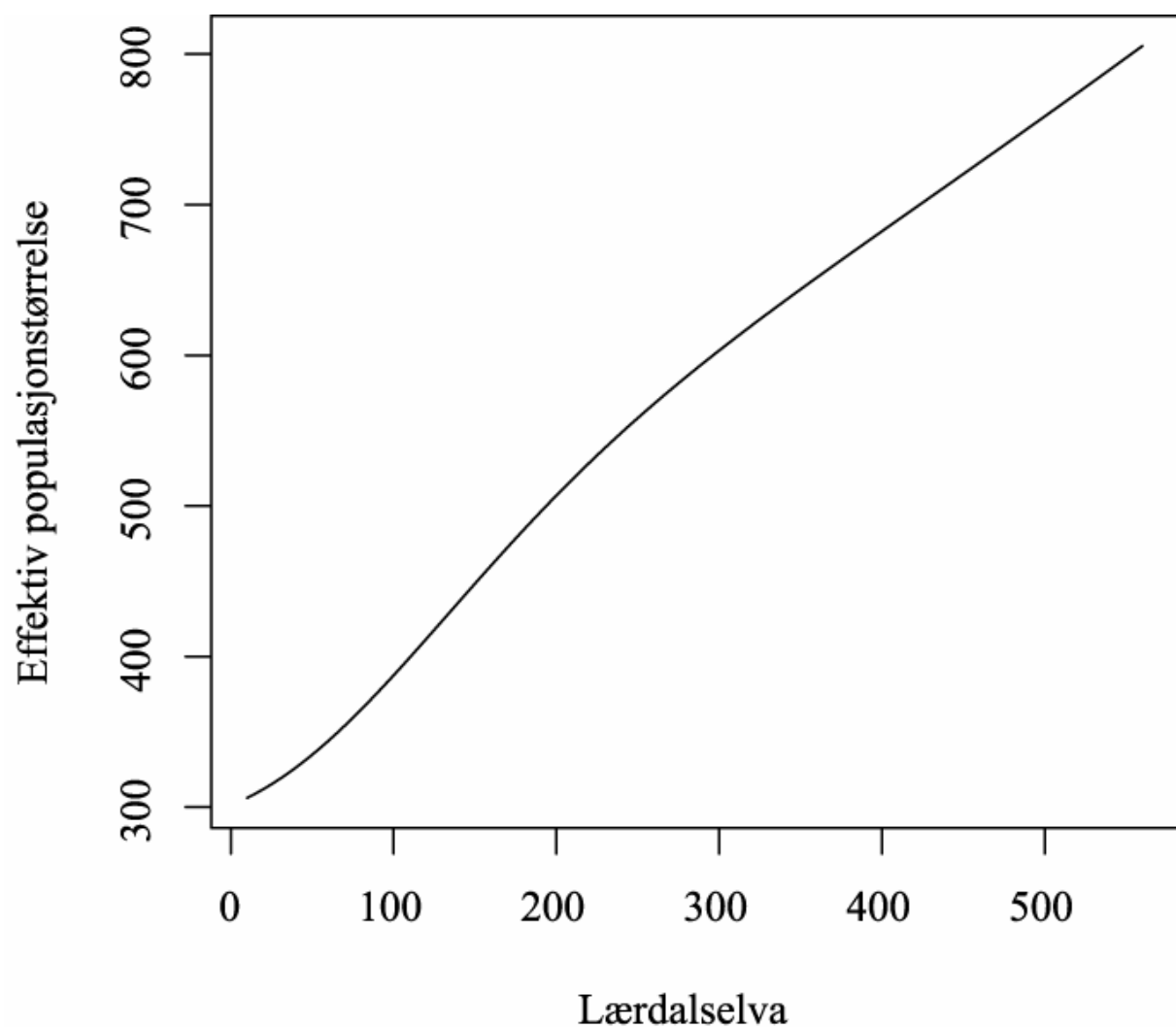
**Figure 2** suggests that in this source-sink system, the total effective size is an almost linear function of the effective size in the Lærdalselva. The effect of increasing the population size in the Lærdalselva from 0 to 540, suggests an additive increase in the total effective size from around 310 to 780 for the whole system.

***Effect of protecting sink populations.*** The small number of anadromous spawners in some of the rivers in the Sognefjorden has recently motivated local protection of spawning populations by prohibiting rod fishing in the river. Based on local counts of spawners and catch statistics, this would be equivalent to doubling the spawning population size of some of the smaller populations (Sættem 1995).

One way of evaluating such strategies, apart from looking at the effect on each local population, is to look at how the total effective size of the system of ten rivers is affected by a change in one of them. We have calculated the elasticity,  $e$ , of the estimate of total  $N_e$  with

respect to change in the local population sizes  $N_i$ , that is, the partial derivative of total  $N_e$  with respect to  $N_i$ :

| Pop | $e$               |
|-----|-------------------|
| 1   | 1.01              |
| 2   | 1.19              |
| 3   | 1.19              |
| 4   | 1.15              |
| 5   | 1.19              |
| 6   | 1.38              |
| 7   | 0.78 (the source) |
| 8   | 1.40              |
| 9   | 1.29              |
| 10  | 1.01              |



**Figure 2.** Effective population size for 10 salmon populations in the inner part of the Sognefjord, western Norway, as a function of the effective size of the River Lærdalselva population.

We see that a reduction in total effective size is least sensitive to a change in population 7 ( $e = 0.78$  for River Lærdalselva, the source), and most sensitive to change in some of the sink populations ( $e = 1.40$  for population 8, the River Aurlandselva and  $e = 1.38$  in population 6, the River Utlei). Why these particular sink populations have the largest incremental effect, is not currently known, but depends on the details of the (constructed) migration matrix. We can see, however, that  $e \geq 1$  for all the sink populations in the system.

## Discussion

For genetically sub-structured species, it is important to determine which populations or other units below the species level that deserve special attention in management. Several concepts have been introduced to define and characterise such units. The most important concepts are Evolutionarily Significant Units (for long-term management and conservation), Management Units (for short-term management) and Operational Conservation Units (for management based on biological as well as socio-economic considerations). For each population unit, general methods have been devised to assess their risk of extinction from genetic, demographic and environmental factors (Mace & Lande 1991; Allendorf et al. 1997), as well as to assess the potential contribution of each population unit to the species' evolutionary legacy (Waples 1991).

One problem for applying conservation genetic guidelines to salmon management is that the guidelines have been designed for isolated populations, whereas anadromous populations that exchange migrants are only partially isolated from one another. This means that the level of genetic variation is not only a function of the population size and demography of the local population, but also of the neighbouring populations and of the level of migration (gene flow) between them. Even a few migrants between populations can provide input to reduce the risk of inbreeding and loss of genetic variation but does not contribute much to reduce demographic risks in a local population (Waples 1998).

Harvesting can have a number of biological consequences for natural populations. During recent decades, several of the world's major fisheries have shown significant collapses, and in 1997, the FAO estimated that 60% of the major marine fisheries were either fully exploited or overexploited, some of them even to the point where they were considered 'vulnerable' by IUCN threat categories. Other effects of harvesting include overexploitation of numerically weaker species and populations that are caught as by-catch in the major fisheries, and the selective regime imposed by catching specific components of the population (Ricker 1981; Law 2000).

The genetic diversity of most marine and anadromous fishes has generally been thought to be unaffected by harvesting, because even at "collapsed" total population sizes they are so numerous that changes in diversity are unlikely to occur (Crow & Kimura 1970). However, when a population is reduced from a very large to moderate size, which would have negligible effect on heterozygosity or inbreeding, genetic variation can still be lost, as the population will harbour a lower expected number of alleles per locus (Ryman et al. 1995). This may be significant, for example in some major loci/genes such as the immune response genes (termed MHC, major histocompatibility complex) where adaptability seems to depend on a high number of alleles at a small number of genes. Moreover, in a recent genetic study of a marine fish species, the New Zealand snapper, *Pagrus auratus*, Hauser et al. (2002) showed a significant decline in genetic variation (heterozygosity) during the exploitation history of the

species. One reason why this can occur seems to be related to the effective population size being as much as five orders of magnitude smaller than the census population size from fishery data for this species.

In the system of ten river populations of Atlantic salmon in the Sognefjorden district, western Norway, one river seems to dominate the others with respect to local population size and productivity, and probably acts as a source population for the remaining nine rivers. When varying its population size from 0 to 540, the total effective size varied from around 310 to 780 for the whole system. These figures amount to rates of inbreeding (and losses of genetic variation) per generation at 0.16% and 0.06%, respectively, if we apply the relationship  $\Delta F$  (or  $\Delta H$ ) =  $1/(2N_e)$ . With respect to the conservation genetic rules-of-thumb cited above, this system does not seem in danger with respect to immediate inbreeding depression, but will on the other hand, not be considered secure from a long-term evolutionary perspective (if it existed alone).

With the apparently high migration rates between rivers (**Table 2**), we have exemplified a system where local adjustment of harvesting has little incremental effect on the total effective size in comparison to uniform effort harvesting (Tufto & Hindar 2003). In other words, a mixed fishery on these populations in the fjord would have approximately the same effect on the total effective size as an optimal, river fishery, as long as the total number of spawners could be controlled. The results might have been different with other local population sizes and a different migration matrix, for example, if migration rates were typically lower and less dominated by a single river. Even so, this example suggests that the setting of CLs on a river-by-river basis or for an aggregate of several rivers, may have only minor genetic consequences as assessed by total effective size  $N_e$ . In such cases, where  $N_e$  seems not to discriminate among varying options for choosing the best level for setting CLs, the choice needs to be grounded on other considerations (e.g. population dynamics, or operational constraints). For example, S/R-relationships developed for European rivers including the R. Lærdalselva (Prévost et al., in press), seems to dictate a much higher number of spawners in this river than the level observed since the mid 1980s, and one that cannot be deduced from considerations of  $N_e$  alone.

It can be argued that the total effective size of a subdivided population is a too simplistic criterion for contrasting management options, and that other factors such as local number of spawners, local inbreeding depression (Lynch 1991) and local demographic and environmental stochasticity (Lande et al. 1999) need to be included. In addition, subpopulations may show genetic adaptations to local environments, such as timing of return to a particular river or tributary (Stewart et al. 2002). The relationship between absolute numbers of spawners and effective population size can also change as a population is harvested. In principle, it is possible to incorporate such processes into the modelling framework of Tufto & Hindar (2003). However, a fundamental difficulty is how to evaluate effective size against harvesting yield or losses arising from other processes. This would require more precise knowledge about how reductions in local effective population size translates into reduction in population viability and productivity.

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