

**Genetic Introgression of the Domestic Atlantic Salmon  
Genome into Wild Populations: A Simulation of  
Requirements for Conservation**

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## ABSTRACT

A model was developed to explore the effects that escaped, farmed Atlantic salmon interacting and mating with wild Atlantic salmon could have on the genome and viability of a known wild population. The proportion of escapees spawning, degree of assortative mating, and degree of adaptive differentiation could be varied. After interbreeding occurred, offspring that survived rapidly replaced the pure wild genome or lineage in the population. The survival of these backcrosses was a function of mean genetic introgression of the domestic genome from farmed fish into the population. Model predictions were sensitive to variability in the probability of mating between escapees and other groups, the relative survival of offspring having received some farmed genome, and the number of mature escapees entering a river. In some situations, applying a "hard" natural selection (low relative survival) to offspring with farmed genome (as for distant or differentiated strains) was found to be more beneficial to population persistence than a "soft" selection (as for closely related stocks). The impact of escapees was minimised by early action to eliminate them or prevent them from interbreeding with the wild population. The model identified a need to dramatically decrease response time for applying conservation measures to preserve a low degree of genetic introgression and prevent extinction of the population after escapees were stopped from entering a river, especially at the high proportions of escapees presently found in some rivers. Failure to stop the escape of farmed salmon and their interbreeding with wild salmon resulted in a high mean genetic introgression in backcrosses and eventual extinction of the self-sustaining population. The reported escape of juvenile salmon from commercial hatcheries and their return as spawners of farmed lineage was predicted to greatly accelerate the increase in genetic introgression and to complicate the successful application of conservation measures to preserve the wild population.

## RÉSUMÉ

Un modèle a été élaboré afin d'étudier les effets, sur le génome et la viabilité d'une population sauvage connue, que peuvent avoir des saumons de l'Atlantique d'élevage échappés interagissant et se reproduisant avec des saumons sauvages. La proportion de saumons échappés frayant, le degré d'appariement préférentiel et le degré de différenciation adaptative pouvaient être variés. Après croisement, les descendants qui survivent remplacent rapidement les individus à génome sauvage pur au sein de la population ou de la lignée. La survie de ces produits de rétrocroisement était fonction de l'introgression génétique moyenne du génome des poissons d'élevage au sein de la population. Les prévisions du modèle étaient sensibles à la variabilité de la probabilité d'appariement entre les poissons échappés et ceux d'autres groupes, la survie relative des descendants ayant reçu une partie du génome des poissons d'élevage et le nombre de poissons échappés matures pénétrant dans un cours d'eau. Dans certaines situations, l'application d'un taux de sélection naturelle élevé (survie relative faible) aux descendants possédant le génome de poissons d'élevage (comme pour les souches éloignées ou différenciées) s'est avérée plus utile au maintien de la population que l'application d'un taux de sélection naturelle faible (comme pour des stocks très apparentés). L'effet des poissons échappés était réduit par des mesures hâtives visant à les éliminer ou à les empêcher de se croiser avec des individus de la population sauvage. Le modèle a montré la nécessité de réduire de façon très importante le temps d'intervention pour la prise de mesures de conservation visant à préserver un faible degré d'introgression et de prévenir l'extinction de la population après que l'on ait mis fin à l'introduction de poissons échappés d'élevage dans le cours d'eau, surtout aux taux élevés de poissons d'élevage se trouvant actuellement dans certains cours d'eau. Le fait de ne pas mettre fin à la perte de saumons d'élevage et à leur reproduction avec des saumons sauvages donnait lieu à un taux d'introgression génétique moyen élevé chez les poissons de rétrocroisement et à la disparition éventuelle de la population autosuffisante. Il a été prévu que la perte signalée de saumons juvéniles d'installations commerciales, et leur retour sous forme de géniteurs, accélérerait fortement l'introgression et compliquait la bonne application de mesures de conservation visant à préserver la population sauvage.

## Introduction

The accidental or intentional release of domestic stock into environments where they can interbreed with naturally occurring individuals is rapidly becoming an important consideration in conservation biology (Hindar et al. 1991; Hunter 1996; Beardmore et al. 1997; Knapp and Dyer 1998). Accidental releases of domesticated animals generally do not involve any genetic planning, and the potential for genetic interaction with wild populations can be significant (Hindar et al. 1991; Hunter 1996; Beardmore et al. 1997). The marine environment is perhaps the most common site of accidental introduction of non-native individuals with the two major vectors being commercial shipping and aquaculture (Gaffney and Allen 1992; Carlton and Geller 1993; Carlton and Hodder 1995; Beardmore et al. 1997). The determination of the genetic effects and environmental impacts of these introductions can be very difficult. However, there is agreement that the outcome of potential genetic interactions could be severe, depending on the level of genetic differentiation between the introduced and the native organisms (Rhymer and Simberloff 1996; Beardmore et al. 1997; Meffe et al. 1997; Knapp and Dyer 1998).

Large numbers of farmed Atlantic salmon (*Salmo salar*) escape from sea cages, and the entry of these accidentally released domestic salmon into rivers has become frequent and widespread (Bergan et al. 1991; Lund et al. 1991; Carr et al. 1997a; Sægrov et al. 1997; Youngson et al. 1997; O'Neil 1998). Their migration into freshwater to spawn may create the illusion that wild populations are healthy, but a wide variety of direct ecological and behavioural interactions can occur between farmed and wild salmon throughout their life cycles (see reviews by Jonsson 1997; Lacroix and Fleming 1998). These can lead to negative impacts on the wild population (Bergan et al. 1991; Webb et al. 1991; Lura and Sægrov 1993; Lura et al. 1993), and in the worst cases escaped farmed salmon replaces the original salmon stock (Sægrov et al. 1997).

A critical concern about escaped farmed salmon is related to the potential of intraspecific gene introgression (i.e., the influx of novel genetic variants) resulting from interbreeding between farmed salmon and wild salmon populations (Hindar et al. 1991; Saunders 1991; Økland et al. 1995). This concern stems from the potential genetic divergence of farmed salmon from wild salmon due to domestication and the use of exogenous stock (Hindar et al. 1991; Thorpe 1991; Rhymer and Simberloff 1996). Genetic differentiation between farmed and wild stocks of Atlantic salmon depends upon the origin of the farmed stock introduced into an area. Virtually all genes in farmed salmon stocks are likely to be shared, except where they derive from different continental stock groups (Verspoor 1997, 1998). New farm specific variants are unlikely to have arisen and become common or fixed in the course of the few generations that most farmed stocks have been in culture (e.g., on the East Coast of Canada; Glebe 1998). As with differences between wild populations, differences between farmed and wild salmon stocks are most likely to involve shifts in allele frequencies that cause radical changes to the genotype distributions they each contain. In a study of the performance of wild, farmed, and hybrid progeny in a natural river environment, McGinnity et al. (1997) concluded that farmed salmon could produce long-term genetic changes in natural populations. The effects of such genetic changes due to introgression of genes from escaped domestic stock on the relative fitness and phenotypic variation of native stocks are unpredictable in the short term, but they are likely to produce maladaptive genotypes in the long term (Rhymer and Simberloff 1996; Fleming and

Einum 1997). Maladaptive genotypes could then affect the degree of adaptive differentiation and reduce relative fitness.

The influence of genetic (interbreeding between forms) and non-genetic (increased density) factors on the persistence of native populations was explored in a numerical model by Hutchings (1991). In the absence of empirical data, the model was based on a simple hypothetical population and the main conclusions were intuitively expected: the impact of introduced farmed salmon depended upon their relative numbers, the relative survival of their hybrid and pure offspring, and the frequency of introduction. However, the model was limited by the paucity of data concerning these variables. Such model specifications can have a large impact on conclusions about population persistence (e.g., Burgman et al. 1993). Therefore, genetic models should, whenever possible, be based on empirical ecological and population data for specific target species and populations (Boyce 1992; Hilborn and Mangel 1996). For example, computer simulations of genetic dynamics following hybridisation in a hypothetical population with overlapping generations (such as Atlantic salmon) has indicated that the amount of temporal allele frequency shift is larger than for a population with discrete generations (Ryman 1997). Thus, the assumption of discrete generations will fundamentally alter the genetic predictions of a model and the outcome for a population.

To address some of the limitations of previous models of farmed-wild salmon interactions, we used a case study, the wild Atlantic salmon population in the Magaguadavic River of New Brunswick (Carr et al. 1997a). We used a river- and stock-specific model that tracks through time multiple overlapping generations in a population of Atlantic salmon (Korman et al. 1994) to quantify the outcome. The model operates at the genealogical level, calculating and tracking the numbers of spawners in distinct lineage groups based on their relative proportions of farm and wild ancestry, through interbreeding and backcrossing, and evaluating overall adaptive change (i.e., as reflected by changes in overall numbers in a population). The proportions of farm and wild ancestry possessed by each lineage group determined its relative fitness. This simplification of the genetic processes operating when farm and wild stocks interbreed in the wild was used to make the model more tractable. The wealth of information available for the Magaguadavic River allowed us to parameterise our model to be used for simulation of a well understood biological system that could then act as a "model system" for similar situations with other less well known biological and physical parameters.

## **Materials and Methods**

### **Study Site and Population**

The Magaguadavic River is a river in Atlantic Canada, where the intrusion of farmed Atlantic salmon that escaped from cages has been closely monitored (Carr 1995; Carr et al. 1997a). Historical data describing the wild salmon population have been summarised in Lacroix (1994) and Marshall et al. (1997). The river empties into Passamaquoddy Bay and is at the centre of the Bay of Fundy salmon aquaculture industry in the Fundy Isles area of south-western New Brunswick. A hydroelectric dam with fishway and trap near the river mouth has been used to count all fish entering the system (Martin 1984, 1987). Marine cages for salmon farming are

located throughout Passamaquoddy Bay and the Fundy Isles, and some cages used for early rearing of post-smolts in brackish water until transfer to sea cages are located near the mouth of the river estuary. Three commercial hatcheries that supply about 2 million smolts annually to the salmon aquaculture industry are located along the river.

The river presents a unique opportunity to study interactions between escaped farmed salmon and the wild population (Carr et al. 1997a). Observations have been made since 1980 when salmon farming in the region started (J. D. Martin, Department of Fisheries and Oceans, St. Andrews, pers. comm.) and escaped farmed fish were first found entering the river in the early 1980s (Martin, 1984). At that time, partial annual counts of wild spawners indicated that the wild population probably exceeded 1000 fish (Martin 1984, 1987; Lacroix 1994). Complete counts of farmed and wild salmon have been made continuously since 1992, and the biological characteristics of wild and farmed fish recorded (Carr 1995; Carr et al. 1997a). These data, summarised in Table 1, were used to parameterise our model and to set realistic bounds to the model scenarios.

The majority of the escaped farmed fish entering the Magaguadavic River fail to sexually mature or spawn in the year of entry (see Table 1; Lacroix et al. 1997). Nevertheless, the timing of migration, spatial distribution, and seasonal changes in reproductive function of wild and some farmed salmon in the river indicate that interbreeding can occur (Carr 1995; Carr et al. 1997b; Lacroix et al. 1997). Successful spawning and survival of eggs was confirmed for farmed females (Carr 1995; Carr et al. 1997a). Large numbers of juvenile salmon also escape from hatcheries along the river and emigrate as smolts to potentially return and interbreed with native wild salmon (Stokesbury and Lacroix 1997).

Table 1. Numbers of wild and escaped farmed Atlantic salmon entering the Magaguadavic River during 1992–1996. Numbers of spawners are based on observed evidence of sexual maturation, and total egg deposition was estimated using observed sex ratios, mean fork length and fecundity for females of each age class (one-sea-winter, two-sea-winter maiden and repeat) for wild and farmed spawners separately. All farmed post-smolts were mature anadromous males that escaped and entered the river before spending a winter at sea.

Year	Wild		Farmed				Wild and farmed			
	Total spawners	Total eggs	Total number	% mature	Post-smolts	Total spawners	Total eggs	Total captured	Total spawners	% farmed spawners
1992	293	1,120,102	149	8.7	1	13	26,838	442	306	4.2
1993	237	981,099	154	7.1	2	11	31,337	391	248	4.4
1994	131	460,957	1203	4.3	13	52	68,040	1334	183	28.4
1995	79	153,030	789	9.1	27	72	85,849	868	151	47.7
1996	69	156,812	240	22.1	8	53	101,365	309	122	43.4
Average	162	574,400	507	7.9	10	40	62,686	669	202	19.8

## Model Structure and Function

We developed a simulation model that genealogically tracks different lineage groups of Atlantic salmon spawners over time. The model follows crosses between wild and farmed individuals in the first generation ( $F_1$ ) and backcrosses in subsequent generations. Model predictions of abundance are influenced primarily by the number of escaped farmed spawners entering a river, the extent of mating between the farmed and wild spawners, and assumptions of the survival of genetically introgressed groups relative to fish with a pure wild genome. This interaction model uses a stock-recruitment (S-R) relationship to simulate the population age structure and return rates. The "Atlantic Salmon Regional Acidification Model" (ASRAM), a habitat-based process model which simulates population dynamics at a river-system scale (Korman et al. 1994; Lacroix and Korman 1996), was used to generate the S-R relationship for the Magaguadavic River as there was not sufficient data to generate the relationship empirically.

ASRAM consists of three main submodels (details in Korman et al. 1994): (1) a river-distribution submodel distributes initial egg numbers and the predicted number of returning adults among reaches in a river system on the basis of water surface grade and the area of each reach, (2) a juvenile submodel predicts the numbers of smolts of different ages produced in each reach on the basis of egg density, natural mortality rates, and assumptions of density dependent growth that affect age at smoltification, and (3) an adult submodel predicts the number of adults returning to the river system on the basis of the total number of smolts produced from all reaches, and a fixed maturity and mortality schedule. ASRAM was parameterised to reflect characteristics of the Magaguadavic River and its salmon population over the 1992–1996 period (Carr 1995; Carr et al. 1997a). An estimate of  $9.33 \times 10^6 \text{ m}^2$  of habitat, determined by remote sensing (see Amiro 1993 for method details), was used as input to the model. Empirical estimations of emergence mortality rate (Peterson 1978), parr and smolt sizes (Stokesbury and Lacroix 1997), ratio of average smolt ages (Martin 1984; J. Carr, Atlantic Salmon Federation, St. Andrews, unpubl. data), and marine mortality rate (P. Amiro, Department of Fisheries and Oceans, Halifax, unpubl. data) were used to parameterise the model. ASRAM was used to simulate recruitment across a range of input spawner abundance to generate the S-R relationship. This relationship, with an equilibrium population of 3,000 spawners at full carrying capacity, uses the total number of spawning adults to predict the total returns of spawning adults at the age of maturity within our genetic interaction model (Fig. 1). The S-R relationship predicted by ASRAM can be reproduced by the Beverton-Holt relationship:

$$\text{Recruitment} = \frac{6823 * \text{Spawners}}{3652 + \text{Spawners}} \quad (1)$$

The interaction model tracks the abundance of four groups of potential spawners: (1) wild fish with no genetic introgression from farmed stock, (2) farmed fish escaped from aquaculture operations, (3) farmed  $F_1$  fish ( $F_{1\text{farm}}$ ) for which one or both parents were escaped farmed fish, and (4) backcrosses for which neither parent was an escaped farmed fish but for which at least one parent was not of wild stock (Fig. 1). We define the term "wild" fish as pure wild lineage or genetic stock over all previous generations (i.e., no introgression of farmed genome). The terms "farmed" or "escapee" refer to escaped farmed stock only; thus if two farmed fish produce

offspring, these animals would be  $F_{1farm}$  upon sexual maturation. These  $F_{1farm}$  are considered separately in the model because they will have undergone some natural selection and no longer represent the same gene pool as first generation farmed fish that escaped. Therefore, mating among the four spawner groups results in only three types of offspring: (1) wild, (2)  $F_{1farm}$ , and (3) backcrosses (Table 2). The backcrossed fish are animals that are the product of at least two generations of selection but have at least some introgressed farmed fish genes.

Table 2. Possible crosses among Atlantic salmon spawners of different origin in the Magaguadavic River and resulting genome types as used in the model.

Male parent	Female parent			
	Wild	Farmed	$F_{1farm}$	Backcrossed
Wild	Wild	$F_{1farm}$	Backcrossed	Backcrossed
Farmed	$F_{1farm}$	$F_{1farm}$	$F_{1farm}$	$F_{1farm}$
$F_{1farm}$	Backcrossed	$F_{1farm}$	Backcrossed	Backcrossed
Backcrossed	Backcrossed	$F_{1farm}$	Backcrossed	Backcrossed

The model begins a simulation with a fixed number of escaped farmed spawners and the wild population at the estimated full carrying capacity of wild spawners ( $N = 3000$ ). It then proceeds to compute annually the proportion of the three different crosses in each year based on the relative abundance and fecundity of the four spawner types (Table 2) and assumptions of the degree of interaction on the spawning grounds. The number of farmed fish that escape annually can be introduced according to different scenarios (e.g., constant introductions over the duration of the simulation or spike introductions at intervals). A mating selectivity factor ( $MS$ ) is applied (as shown in Fig. 1) to adjust the extent to which escaped farmed spawners will mate with spawners that originated from the river (wild,  $F_{1farm}$ , and backcross). This parameter incorporates factors (behavioural, physiological and genetic) potentially affecting mating between escaped farmed and other spawners (Webb et al. 1991; Fleming et al. 1996; Fleming and Einum 1997). We assumed that spawners which originate from the river, and thus have experienced at least one generation of selection, but are not of pure wild genome ( $F_{1farm}$ , or backcross) will exhibit similar migration timing and distances and spawning behaviour to pure wild fish.  $MS$  controls the frequency of mating between returning spawners (pure wild,  $F_{1farm}$ , and backcross genomes) and escaped spawners (farmed genome), which in turn affects the availability of these genomes to interact in other mating combinations (Table 2). The probability of a mating occurrence between two genomes ( $Prob_M$ ) is dependent on the proportion of each genome type ( $Prop_{gx}$ ) relative to the total number of spawners and  $MS$  such that:

$$Prob_M = Y * (Prop_{g1} Prop_{g2}) (1 - MS) \quad (2)$$

in the case that  $g1$  = pure wild genome and  $g2$  = farmed genome, or

$$Prob_M = Y * (Prop_{g1} Prop_{g2}) (1 + MS) \quad (3)$$

in the case that  $g1 = g2$  and is pure wild or farmed genome, or one of the genomes is  $F_{1farm}$  or backcrossed and the other can be any genome except farmed.  $Y$  is a multiplier equal to one when  $g1 = g2$ , or 2 when  $g1 \neq g2$ . When  $MS = 0$ ,  $Prob_M$  is totally dependent upon the relative number of spawners of each genome. When  $MS = 1$ , there will be no mating between farmed and pure wild genomes ( $Prob_M = 0$ ). As a reference point,  $MS = 0.7$  was estimated for the Magaguadavic River based on the degree of spatial overlap during spawning between wild and escaped farmed spawners using migration timing and distances for both types of spawners in the river (Carr 1995; Carr et al. 1997a, 1997b).

The number of eggs per mature spawner (both sexes) of each type (3000 eggs per wild spawner, 2000 eggs per farmed spawner) was used as a weighting factor to compute the proportion of progeny in the three offspring types according to the 16 possible crosses (Table 2). This was based on total egg contributions (Table 1) calculated separately for wild and farmed spawners from their respective maturity schedule, size-at-age, sex ratio, and fork length during the 1992–1996 period (Carr et al. 1997a), and a fecundity – fork length relationship developed by Marshall and Penney (1983). The low proportion of female farmed spawners (0.42), a function of the presence of farmed post-smolts which were all mature males (Table 1), was largely responsible for the large difference in eggs per spawner between wild and farmed fish.

Our stock-recruitment relationship derived from ASRAM assumes that density dependence occurs in the juvenile life stages rather than during spawning. Because ASRAM was parameterised using wild stock characteristics that control the average egg contribution per spawner, all spawners used as input to the S-R relationship are assumed to exhibit these wild stock characteristics. Because farmed and wild mature spawners have different numbers of eggs, we standardised the number of escaped farmed spawners into equivalent wild units by computing an effective number of farmed spawners ( $EFS$ ) using:

$$EFS = FS * EMS_{farm} / EMS_{wild} \quad (4)$$

where  $FS$  is the number of farmed spawners, and  $EMS$  is the eggs per mature wild or escaped farmed spawner. Because the number of eggs produced by farmed spawners was 2/3 that of wild spawners, the effective number of farmed spawners was then equal to 2/3 the total number escaping to the river.

In each year, the simulated total number of spawners of each of the three offspring types and the number of effective escaped farmed fish are used as input to the S-R relationship to predict the numbers of recruits returning to the river in subsequent years (Fig. 1). The time lag between spawning and recruitment reflects the age-at-maturity schedule of the wild population (incorporated in Table 1). Recruitment is then divided into the three offspring types based on the proportions of progeny of each type determined in the brood year and adjusted for each genome type as a function of the mean genetic introgression in each type using:



$$RS_x = 1 - \frac{GI_x^{sl}}{K_{half}^{sl} + GI_x^{sl}} \quad (5)$$

and

$$Recruitment_x = f(S-R) * RS_x \quad (6)$$

where  $RS_x$  is a relative survival multiplying factor used to reduce the recruitment for genome type  $x$  predicted by the S-R function  $f(S-R)$ ,  $K_{half}$  is the mean genetic introgression level (0–1) for the genome type which reduces the recruitment rate predicted by the S-R function by 50%, and  $sl$  is an exponent which controls the slope of the  $RS_x$  relationship. Note that when  $GI_x = 0$  (wild genome type),  $RS_x = 1$ , and recruitment is predicted solely as a function of the S-R relationship for wild fish.

The basis for this  $RS_x$  index is that an increase in the introgression of domestic genome into wild populations will lead to a decrease in evolutionary potential (Hunter 1996; Rhymer and Simberloff 1996; Meffe et al. 1997; Knapp and Dyer 1998) and affect the viability of the population (Hindar et al. 1991; Hutchings 1991; Saunders 1991; Beardmore et al. 1997). The value of  $RS_{bkx}$  would then depend on the genetic distance between the wild and farmed stocks and on the degree of genetic introgression in backcrossed individuals. For example, to simulate “hard” natural selection pressures on fish with introgressed domestic genome,  $K_{half}$  is set at 0.2 (where an introgression level of 20% reduces the recruitment rate by 50%). To simulate “soft” natural selection,  $K_{half}$  is set at 0.8 (80% introgression required to reduce recruitment by 50%). A default slope value of  $sl = 2$  was used in all simulations as a conservative value to define the shape of the  $RS_x$  relationship for the Magaguadavic River. This was partly based on the only study to date to determine the relative survival of farmed and wild  $F_1$  offspring in a natural environment ( $RS_{F1farm} \cong 0.8$ , McGinnity et al. 1997).

Therefore, to address how genetic introgression from farmed fish into the wild population affects relative fitness, we calculated the mean genetic introgression ( $GI_x$ ) of farmed salmon genome into the population. For each genome type,  $GI_x$  is computed based on the probability ( $Prob_M$  from Eq. 2 and 3) of all possible crosses ( $MaxCrosses$ ) defined in Table 2, and the mean introgression of the parental spawner groups involved in the crosses ( $GI_f$  or  $GI_m$  for female and male parents, respectively). The contribution of each cross to the mean introgression of the genome type is weighted according to the eggs per spawner of the female parent ( $W_f$ ), and  $GI_x$  is calculated using:

$$GI_x = \frac{\sum_{i=1}^{MaxCrosses} W_f * Prob_M * \frac{GI_f + GI_m}{2}}{\sum_{i=1}^{MaxCrosses} W_f * Prob_M} \quad (7)$$

For crosses involving one or two pure wild genome parental groups,  $GI_f$  and/or  $GI_m = 0$ . For crosses involving one or two escaped farmed parental groups,  $GI_f$  and/or  $GI_m = 1$ . For crosses involving  $F_{1\text{farm}}$  and backcrossed (bkx) parental groups,  $GI_f$ ,  $GI_m = GI_{F_{1\text{farm}}}$  or  $GI_{\text{bkx}}$  computed from the spawning event in the previous generation. Mean genetic introgression in the total population is then the sum of  $GI_x$  multiplied by the number of spawners ( $N_x$ ) for each offspring type as a proportion of total population size.

The genetic introgression component of the model represents a simplification of the reality. Introgressive hybridisation normally refers to the addition of genes from one species to the gene pool of another species through hybridisation and backcrossing. At the intraspecific level and in a population genetics framework, genetic introgression generally refers to the influx of novel genetic variants at specific loci. Such fixed differences between the farm and wild stocks will exist where stocks have been derived from different continental groups of Atlantic salmon (e.g., the European strains used in Maine around the Fundy Isles and proposed for use in south-western New Brunswick). Strains with European genetic influences (e.g., Norwegian “Landcatch” strain and other strains from Norway and Scotland) now account for approximately 30–50% of production fish in Maine (Baum 1998). However, widespread fixed adaptive allelic differences are not expected where both the wild and farmed stocks are local (e.g., the Saint John River stock used exclusively in New Brunswick salmon farms). What will most likely occur is that allele frequencies will change as a result of differences in the frequencies of alleles in the farmed and wild groups and the genotypes in the population will change as determined by recombination and gamete assortment. This will occur because, under different selective pressures (i.e., domestication), allele frequencies will change and combinations advantageous for an environment may be lost in the local stock. Genetic introgression could then lead to strong selective pressures on the wild population depending upon the extent of introgression.

The model tracks genealogical introgression using the proportional contribution of each lineage group (i.e., ancestry) to the wild population genome. It is not an allele-based model and does not operate at the gene or locus level. We chose to look at the genome as a unit instead of approaching the issue on an individual locus basis and trying to justify explicit model functions for individual locus interactions. The model does not try to follow allele frequency differences or the introduction of novel genetic variants but instead considers quantitative traits, with the expectation of epistasis and other gene interactions (e.g. co-adapted gene complexes). Our introgression index reflects the probability that the introgression will affect an important gene or trait for the long-term survival of the population. On the basis of functional loci associated with quantitative traits, the model assumes that there will be hybrids (see Table 2), even if the two stocks differ at only one locus. The model does not assume that all genealogical hybrids will have a similarly reduced fitness. Within a population of hybrids, some will, by chance get “dealt” worse genetic mixtures (i.e., lower fitness), while some will get better genetic mixes (i.e., better fitness), but on average there will be a certain amount of reduced fitness characteristic of the level of introgression ( $RS_x$  variable within the model). For computational purposes, the model assumes that selection will not change a backcrossed population to wild if the source of farmed genome is removed (i.e., it does not restore genetic purity and reset genetic introgression to zero). This assumption is realistic if novel genetic variants (i.e., from European strains) were introduced and fixed in the population. However, selection for quantitative traits in domesticated local stocks would not lead to fixation and should be reversible. Hence, care is advised in

interpreting the effects of mitigation for conservation when evaluating the ability to restore a wild population after genetic interaction with a domesticated local stock. The fitness depression of low levels of introgression could be effectively countered by natural selection under those circumstances.

### Impact Simulations

Scenarios were selected to demonstrate the range of model behaviour under continuous annual introductions of farmed spawners, (i.e., where containment problems at cage sites are widespread and chronic). These included simulations with combinations of: (1) low interbreeding between farmed and wild spawners or high mating selectivity ( $MS = 0.8$ ), (2) high interbreeding or low mating selectivity ( $MS = 0.2$ ), (3) “soft” natural selection or high relative survival of  $F_1$  and backcrosses ( $K_{\text{half}} = 0.8$ ), and (4) “hard” natural selection or low relative survival ( $K_{\text{half}} = 0.2$ ). We initially kept the level of introductions constant at the average value in the Magaguadavic River (proportion of spawners of farmed origin in Table 1,  $PS_{\text{farm}} = 0.2$ ) in each simulation to facilitate interpretation and comparison of impacts on the wild population. Additional simulations of these scenarios were then repeated using a moderately high proportion of escapees ( $PS_{\text{farm}} = 0.6$ ) to further explore and summarise model behaviour.

In reality, the proportion of farmed spawners in the river tended to vary considerably from year to year (Table 1). To demonstrate the effects of this variability in the number of escapees and farmed spawner introductions, we ran multiple simulations at different levels of escape of farmed salmon over the observed range ( $PS_{\text{farm}} = 0.05\text{--}0.5$ ) while keeping other variables at default levels for the Magaguadavic River ( $MS = 0.7$ ,  $K_{\text{half}} = 0.8$ ).

For all simulations, model output tracked two types of indicators over time: (1) the numbers of returns ( $N_x$ ) in each of the four spawner groups, and (2) the mean percent introgression of farmed genome ( $GI_x$ ) in each of the three genome groups (Table 2).

### Mitigation Simulations

The model was used to generate scenarios that could be used to define requirements for recovery or persistence of a population that has interacted with escaped farmed salmon as in the Magaguadavic River. Various approaches such as improved containment of farmed salmon at cage sites, sterilisation of farmed fish, the widespread use of triploid production stock (i.e., sterile fish), or the harvest of farmed fish at the river mouth could be used to stop or reduce farmed spawner introductions (Hansen and Youngson 1998). Two model indicators of population performance,  $GI_{\text{bkx}}$  and  $N_{\text{bkx}}$ , were used to assess the effects response time to stop farmed spawner introductions ( $PS_{\text{farm}} = 0$  at  $t+x$ ). Simulations were repeated at fixed continuous introductions over a wide range ( $PS_{\text{farm}} = 0.1\text{--}0.8$ ) and run to 50 yr after introductions were stopped. The Magaguadavic River default values ( $MS = 0.7$ ,  $K_{\text{half}} = 0.8$ ) were used for other parameters. We used a distance-weighted least-squares smoothing procedure to plot isopleths of these performance measures (Wilkinson 1992).

## Results

### General Model Behaviour

Continuous introductions of farmed Atlantic salmon in the Magaguadavic River, the result of escapes from multiple cage sites in the Fundy Isles area every year, invariably resulted in the loss of the pure wild lineage in the population when interbreeding occurred regardless of the scenario (Figs. 2 and 3). The rate at which this loss occurred depended on the extent of interbreeding which in turn affected the fitness (relative survival) of the offspring. The returning spawning population eventually comprised only  $F_{1farm}$  and backcrossed individuals with each group having a different mean level of genetic introgression that changed over time. The number of  $F_{1farm}$  returning to spawn and the mean genetic introgression of this group were related to the annual input of spawners of farmed genome (escapees). With continued input of farmed spawners and interbreeding, backcrosses eventually made up the bulk of the population and decreased over time. In the interim, the maintenance of a spawning group of backcrosses relied on recruitment which determined the population size based on the extent of continued interbreeding with escapees, degree of genetic introgression, and the survival relative to the S-R relationship. Genetic introgression in backcrosses followed specific phases over time: (1) it was zero until the first returning  $F_{1farm}$  fish spawned; (2) it jumped to an initial peak with the first set of backcrosses because they had at least one farmed grandparent (i.e., every backcrossed fish contained at least 25% farmed genome); (3) it then declined over a period of several years to several decades, even though the proportion of pure wild spawners was declining during that time, because many backcrosses were returning with a only small amount of farmed genome causing the mean to decline relative to the initial peak as these backcrossed fish mated with returning wild and  $F_{1farm}$  fish; (4) it finally increased over time after the pure wild lineage disappeared and with a steady input of escaped farmed spawners, and; (5) in some scenarios, it reached a level high enough to result in extinction of a population that was not entirely supported by escapees.

The wide range of scenarios simulated in Figs. 2 and 3 allowed us to examine the sensitivity of model indicators ( $N_x$  and  $GI_x$ ) to large variations in the probability of mating ( $MS = 0.2, 0.8$ ) and relative survival ( $K_{half} = 0.2, 0.8$ ) parameters. We found a need to assess their impact on model predictions because of the paucity of empirical data to support default values. Accurate determination of  $MS$ , which controls assortative mating and the extent of interbreeding between escaped farmed spawners and other spawners, appears to be especially important for the prediction of mean introgression level and persistence of a self-sustaining population. When the probability of mating increased (i.e., as  $MS$  decreased from 0.8 to 0.2), mean  $GI_{bkx}$  increased at a faster rate; by the time  $GI_{bkx}$  reached 100% at low  $MS$ , it was still near its lowest value at high  $MS$  (cf. Figs. 2 and 3 at  $PS_{farm} = 0.2$ ). As a result, the population of backcrosses became extinct within 50–100 yr with high interbreeding (low  $MS$ , Fig. 2), especially with low relative survival (low  $K_{half}$ ). During the same time period, the population persisted at some level below carrying capacity when interbreeding was low (high  $MS$ , Fig. 3). In the long term ( $> 150$  yr), mean  $GI_{bkx}$  eventually increased to 100% and the population disappeared even with low interbreeding because of the continued input of farmed genome by escapees.

The use of “soft” and “hard” natural selection (relative survival) scenarios in these simulations revealed some interesting model behaviour that affected predictions. At a high level of interbreeding ( $MS = 0.2$ ), “hard” selection pressures (low  $K_{half}$ ) caused  $GI_{bkx}$  to jump to 100% in the space of a few years, whereas the rate of increase in  $GI_{bkx}$  was more gradual under “soft” selection (high  $K_{half}$ ) (Fig. 2). Under “hard” selection, the population of backcrossed spawners became extinct shortly after the pure wild stock disappeared. A “soft” selection allowed a small population of backcrosses to persist after 50 yr, but it disappeared soon afterwards with continued input of escapees with farmed genome. Interestingly, the opposite effect was observed for variations in relative survival at a low level of interbreeding. “Hard” selection allowed mean  $GI_{bkx}$  to increase more slowly and to remain lower and the backcrossed population to be more abundant at any given time within the first 150 yr than a “soft” selection (Fig. 3). This could have important implications in the selection of strains used for salmon farming. Their relative fitness when released into the wild could influence the choice of strategy for the preservation of wild stocks.

Table 3. Summary of model exploration of the effects of proportion of farmed spawners, degree of interbreeding, and degree of relative fitness on the viability of a wild Atlantic salmon population. Scoring: decline (-), slow to rapid increase (+ to ++++), stable or gradual change ( $\rightarrow$ ). Years until population loss are approximate and for relative comparison among cells.

	<i>Low Fitness</i>		<i>High Fitness</i>	
	<i>Low Escapees</i>	<i>High Escapees</i>	<i>Low Escapees</i>	<i>High Escapees</i>
<b><i>Low Interbreeding</i></b>	Introgression Rate - / + $\rightarrow$ / ++++	Introgression Rate + / +++	Introgression Rate + $\rightarrow$	Introgression Rate ++++
	Population Loss Wild 70 yr Total 190 yr	Population Loss Wild 25 yr Total 30 yr	Population Loss Wild 35 yr Total 160 yr	Population Loss Wild 20 yr Total 40 yr
<b><i>High Interbreeding</i></b>	Introgression Rate - / ++++	Introgression Rate ++ / ++++	Introgression Rate +++	Introgression Rate ++++
	Population Loss Wild 50 yr Total 60 yr	Population Loss Wild 20 yr Total 30 yr	Population Loss Wild 25 yr Total 75 yr	Population Loss Wild 15 yr Total 35 yr

Additional simulations of scenarios shown in Figs. 2 and 3 ( $PS_{\text{farm}} = 0.2$ ) using a moderately higher proportion of escapees ( $PS_{\text{farm}} = 0.6$ ) indicated that variation in  $PS_{\text{farm}}$  greatly affected model predictions (summarised in Table 3 as low and high escapees). A high  $PS_{\text{farm}}$  had the greatest impact on the rate of introgression resulting in population loss within 40 yr at low and high fitness or low and high interbreeding. This impact occurred even at low interbreeding (high  $MS$ ) because mating selectivity in the model only affects interactions between escaped farmed fish and other groups of fish;  $F_{1\text{farm}}$  and backcrossed spawners returning with wild fish are scheduled to continue mating together and with the wild fish proportional to their relative abundance and, thereby, continue to impact the wild population. Therefore, the degree of interbreeding had a high impact only when the proportion of escapees was low. A high proportion of escapees rapidly erased the benefits of low interbreeding. A low fitness of farmed and hybrid offspring greatly delayed the impacts, allowing time for conservation measures to be applied. However, the benefits of low fitness for farmed offspring would disappear if the proportion of escapees and interbreeding with the wild population were high.

### Forecasts for the Magaguadavic River

The proportion of escaped farmed spawners reported for the Magaguadavic River ( $PS_{\text{farm}} = 0.05\text{--}0.5$ ) had a large influence on the rate at which  $GI_{\text{bkx}}$  increased in the resulting population (Fig. 4). This would similarly affect the relative survival of offspring and persistence of a self-sustaining population in the river. After only 30 yr of farmed spawner introductions,  $GI_{\text{bkx}}$  could be  $< 5\%$  at the lowest introduction level ( $PS_{\text{farm}} = 0.05$ ) and  $> 90\%$  at the highest level ( $PS_{\text{farm}} = 0.5$ ). This would lead to large difference in the ability of a population to survive in the river. At  $PS_{\text{farm}} = 0.5$ , pure wild spawners decreased to  $< 1\%$  in 21 yr, and backcrossed spawners disappeared within 40 yr, by which time the entire population was dependent upon the annual input of escaped farmed spawners. In contrast, at  $PS_{\text{farm}} = 0.05$ , pure wild spawners decreased to  $< 1\%$  in 44 yr, and backcrossed spawners were still at carrying capacity after 100 yr. A change in maturation rate of escaped, farmed salmon would have the same impact. Figure 4 also demonstrates the potential usefulness of controlling the entry or spawning of escaped farmed salmon in the river as a management action to preserve a population of wild (albeit backcrossed) spawners with a relatively low  $GI_{\text{bkx}}$  until an effective solution can be developed and applied to the general problem of escapees.

Based on the general behaviour of the model described, the high mating selectivity calculated for the Magaguadavic River ( $MS = 0.7$ ) would allow a population to persist with a relatively low mean  $GI_{\text{bkx}}$  at introduction levels ( $PS_{\text{farm}} = 0.2$ ) that would otherwise rapidly lead to the loss of the population extinction at lower  $MS$  values. However, the high fitness of farmed offspring hypothesised for the Magaguadavic River, based on the close genetic distance between the farmed (Saint John River origin) and wild stocks ( $K_{\text{half}} = 0.8$ ), would have a greater negative impact on mean  $GI_{\text{bkx}}$  and population size after 50 yr than if a “hard” selection was applied (representing a distant strain or domesticated stock developed to be unfit for survival in the wild) (as in Fig. 3).

### Mitigation Required for Conservation

Options for removing the introduction of farmed spawners (escapes) into the breeding population of wild fish, if applied successfully, would be equivalent to stopping the introductions at time  $t+x$ , but would obviously have no effect on the impact accumulated from introductions of farmed fish up to that point. The level of  $GI_{bkx}$  reached at time  $t+x$  would then be of utmost importance for the persistence of a salmon population not supported by escapees. Simulations showed that, after the introduction of farmed spawners was stopped ( $PS_{farm} = 0$ ,  $t+x = 50$  yr), the total standing stock of recruits immediately declined to a lower equilibrium dictated by the mean  $GI_{bkx}$  level reached at time  $t+x$  (Fig. 5). However,  $GI$  did not return to zero as in the pure wild lineage (see model assumptions on p. 9). Therefore, if introductions were stopped early, when  $GI_{bkx}$  is low, a healthy population of backcrosses would persist after the loss of the pure wild genome, and population extinction could be avoided. However, if the delay in preventing escapes or restricting introductions and interbreeding allowed  $GI_{bkx}$  to increase beyond a threshold (which is a function of other variables in the model), or if the level of farmed spawner introductions was high enough (e.g.,  $PS_{farm} = 0.4$  in Fig. 5) at a given  $t+x$ , the population would still decrease to extinction at some time thereafter; the rate at which this decrease occurred was a function of  $GI_{bkx}$  at  $t+x$ .

The hypothetical scenario of applying conservation measures and resolving the problems of farmed salmon containment at cage sites adjacent to the Magaguadavic River, when simulated over a range of introduction levels ( $PS_{farm} = 0.1-0.8$ ), indicated that immediate action was critical to effective management and stock preservation (Fig. 6;  $GI_{bkx}$  and  $N_{bkx}$  at time  $t+x+50$  yr). After farmed fish had interacted with the wild population, the pure wild genome could not be preserved, but halting introductions as soon as possible within the first 20 yr would ensure the persistence 50 yr later of a wild, self-sustaining spawning population of backcrosses at  $PS_{farm} < 0.5$  (Fig. 6). The isopleths in Fig. 6 begin to approach vertical as more time is taken to act in stopping introductions, indicating that  $PS_{farm}$  then had a bigger effect on the population size than the year introductions were stopped. Dealing with the problem of escaped farmed fish early (i.e., in less than 20 yr) resulted in a lower mean  $GI_{bkx}$  in the population, and made an especially large difference at moderately high introduction levels (where more isopleths are crossed by a vertical line in Fig. 6). For example, at  $PS_{farm} = 0.5$ , mean  $GI_{bkx}$  did not exceed 50% if introductions were stopped in 5 yr, but waiting only 20 yr to take action resulted in a mean  $GI_{bkx} > 75\%$  50 yr later and in the extinction of the population. At a lower  $PS_{farm}$  (0.2), conservation action could be delayed longer before mean  $GI_{bkx}$  exceeded 25% or the population size decreased substantially. This is also shown by the comparison of model indicators over time at  $PS_{farm} = 0.2$  and 0.4 in Fig. 5. The use of different model parameter values, other than the default, would modify the conservation requirements slightly in line with the behaviour of the model described in Figs. 2 and 3, but the need for immediate action would remain as a requirement for preventing population extinction.

## Discussion

Our model showed that, after escaped farmed salmon entered a river and interbred with the wild population, salmon with the endemic pure wild genome rapidly disappeared and the level of genetic introgression in the population of backcrosses determined the fate of that population. The time and rate at which events occurred depended, in order of importance, upon: the number of escapees and type of introduction, the extent of interbreeding, and the relative survival of offspring with some farmed genome. However, the loss of the pure wild genome did not imply that a self-sustaining wild population would necessarily disappear, provided that some management action was taken to stop escaped farmed spawner introductions. The timing of conservation measures would dictate the fate of the population. Thus conservation biologists would be faced with a dilemma; the population could appear to be doing well (and conceal the need for immediate action) while it was driven to "extinction by hybridisation and introgression" (Rhymer and Simberloff 1996). Ultimately, the adaptability of the population to natural environmental variation and its potential long-term resilience would still be compromised by the genetic introgression of farmed salmon genes (Hindar et al. 1991; Hutchings 1991; Saunders 1991; Beardmore et al. 1997). This assumes that the wild and farmed salmon are under different selection pressures, and that the genes that are most relevant to those selection pressures will differ. Thus, our inclusion of mean genetic introgression by lineage (genetic type) as a primary indicator within our model added a new dimension to modelling the impact of interactions between farmed and wild populations that was lacking from previous simulations (Hutchings 1991). Our explicit inclusion of genetic factors in controlling relative survival in the model improved our ability to interpret interactions between farmed and wild fish in nature (Bentsen 1991; Mork 1991).

Our exploration of model behaviour revealed that, under some conditions, the use of strains of salmon poorly adapted to survive under local conditions (i.e., with high genetic distance to the wild stock) could lead to lower genetic introgression and greater chance of persistence in the population of backcrosses returning to spawn as wild fish (see scenarios of "hard" selection). Genetic distance measures are often used to quantify genetic differentiation between artificially reared and wild populations (e.g., Cross and King 1983; Stahl 1983; Garcia-Marin and Pla 1996; see Smith and Wayne 1996). A closely related strain (e.g., the domesticated Saint John River strain used for farming in New Brunswick), with an assumed better relative survival (see scenario of "soft" selection) would lead to greater genetic introgression over time and could erode genetic differentiation. Genetic distance of the backcrossed population from the pure wild lineage would continue to increase if no action was taken to stop the introductions of escapees into the spawning population.

It is important to make the distinction between year-to-year survival and long-term fitness; our relative survival ( $RS_x$ ) index reflected expected differences in short-term fitness of progeny with some farmed salmon genome in a natural environment. Despite this survival cost, the constant intrusion of farmed fish into the system resulted in a presence of recruits proportional to the introduction level and a new, initially higher, population size. The increase in yield could falsely be perceived as a benefit in a river with a dwindling population of wild salmon (from other unrelated causes). However, this short-term population increase would come at the cost of significant levels of introgression of the farmed genome into the wild population. Only upon



stopping introductions were the true costs of genetic introgression clearly observed by modelling; the population rapidly became extinct if genetic introgression had increased beyond a threshold. This indicated that long-term fitness of the population would be better represented by the level of genetic introgression rather than by the size of the population, an important point to remember when making management decisions.

It was evident from model simulations that prevention of any farmed salmon introductions was the only means of safeguarding the wild genome. If this was not possible, then the best conservation strategy would be to keep genetic introgression in the population as low as possible. Dealing with the problem of escaped farmed fish early (i.e., in less than 5 yr) resulted in a much lower mean introgression level in the population, especially as the severity of introductions increased. The shape of the isopleths for mean introgression level at different introduction cut-off times (see Fig. 6) indicated that reduced response times for applying conservation measures were critical for the conservation of wild populations with low levels of genetic introgression. Furthermore, our simulations indicated that none of the alternative management strategies that were proposed for dealing with escaped farmed salmon (Hansen and Youngson 1998) would be effective in preventing genetic introgression of farmed fish genes into the wild stock. Supplementing the wild stock using captured wild fish as brood stock was proposed as an interim measure to sustain the wild genome in the population (Ritter 1997); however, rearing the resulting offspring under artificial conditions could introduce different selection pressures and affect the gene pool (Hindar et al. 1991). Better containment at cage sites would decrease the frequency and number of escapees, but this would only change the rate at which events occurred. With continued interbreeding over many years, genetic introgression could eventually increase enough to lead to extinction of a self-sustaining salmon population. Exclusion of escaped farmed fish by removal at a river mouth would be effective only if used at the first signs of interbreeding with the wild population. Partial reproductive exclusion of escaped farmed spawners from the wild population by using barriers to limit upstream migration of farmed fish in a river would have the same effect as increasing mating selectivity (cf. Figs. 2 and 3). The use of sterile fish, such as triploids, in aquaculture would probably be the most effective way of preventing large-scale genetic introgression (Johnstone 1998), but would not remove the potential for ecological interactions (see review by Lacroix and Fleming 1998).

Sensitivity of model predictions to variations in key parameters indicated that, after number of escapees, mating selectivity was the next critical parameter because of its large effect on the introgression dynamics, whereas errors in estimates of relative survival of offspring had comparatively less of an impact (cf. Figs. 2 and 3). Therefore, actions that would significantly reduce the number of escapees or reduce the probability of interbreeding should be considered when making decisions related to conservation of a population interacting with escapees. Mating selectivity between the introduced and native salmon merits further study as a potential site of implementing actions for conservation of a population if the escape of farmed salmon cannot be fully prevented.

Our conclusions for the model system should be interpreted with the knowledge that the results of our simulations were based on very conservative scenarios of farmed fish introduction (low  $PS_{\text{farm}}$ ), low interbreeding (high  $MS$ ), and high relative survival of  $F_{1\text{farm}}$  and backcrossed offspring ("soft" selection or high  $K_{\text{half}}$ ). To keep the model as conceptually simple as possible,

we did not include additional sources of potential escapee impact that have been identified for the Magaguadavic River population. For example, the introduction of farmed fish that are known to escape from hatcheries along the river (i.e., during egg to smolt rearing) and then survive to emigrate as smolts would accelerate the impacts if they were included in the  $F_{1\text{farm}}$  component of the model. By setting the contribution of escaped juvenile fish from hatcheries to 60% of all emigrating juvenile fish (as measured by Stokesbury and Lacroix 1997), and then applying a marine survival rate of only 1.5% for the escaped hatchery fish (Marshall et al. 1997), the model predictions were equivalent to increasing the average  $PS_{\text{farm}}$  from 0.2 to 0.35 in Figs. 5 and 6. This translated into a large increase in the predicted rate of impacts on the population (high genetic introgression and population extinction), and heightened the need for immediate action to preserve the stock. An increase in the observed low rate of sexual maturation of farmed fish (< 20 %; see Table 1), or in the number of farmed spawners would also have significant impacts on predictions for the stock. Relatively few of the farmed salmon entering the river were capable of reproducing that year (Lacroix et al. 1997). and the potential for these farmed fish to mature and spawn the year after entry is unknown (Lacroix et al. 1997). This introduced a potential for a large number of those salmon to mature the following year, because a large number of the immature fish remain in the river (Carr et al. 1997a, 1997b). The inclusion of these potential spawners to interactions in subsequent years would add to the level of farmed fish introduction presently assumed within the model and mean genetic introgression in the population would increase.

A likely alternative scenario to that of continuous introduction of farmed salmon (as in the Magaguadavic River) is a single large escape of farmed fish, resulting from some accident or mechanical failure that affected containment at a cage site, leading to a spike introduction of farmed spawners over two years (because of two potential spawning age classes, Carr et al. 1997a). Model simulation of this scenario, using default values for the model system and a large spike ( $PS_{\text{farm}} = 0.8$ ), showed that even single accidental releases of farmed salmon would have resulted in the replacement of the pure wild genome by a population that consisted of backcrosses with a mean introgression > 50% within 10 yr of the accident and in a reduced recruitment thereafter. The impacts of even a single spike introduction on the population were permanent, with no possibility of return to pre-accident conditions based on the model assumption that the wild population will not have its purity restored through selection.

Our model required the wild population to be at equilibrium (based the on S-R function) when farmed salmon were introduced, thereby building a high level of resilience into the population response. The actual impact of farmed fish introductions would probably occur more rapidly than predicted by the model when the target wild salmon population was at an all-time low, such as in many of the rivers of the Bay of Fundy at present (Amiro and Jefferson 1998; Marshall et al. 1997). The expected impact would also be increased if production of farmed salmon in the Bay of Fundy continued to increase exponentially (e.g., from 6 tonnes in 1980 to more than 32,000 t in 1998 for the Canadian and U.S. waters around the Fundy Isles area alone; Baum 1998; Chang 1998). Furthermore, the potential for escaped farmed fish to stray further to previously unaffected rivers could increase with higher production levels and potentially broaden the interaction to a regional scale.

We have documented here the results of a simulation model designed to illustrate the potential genetic impact of domesticated farmed salmon introductions on wild salmon populations using a case study. The value of the model was conceptual: it indicated that mating selectivity, relative survival, introductions (frequency and magnitude of escapes from farms), and response time to stop introductions were the major determinants of the future of a wild salmon stock exposed to farmed salmon that escape from aquaculture sites. The first two items define areas where immediate research is required to validate and test model predictions, the latter two define monitoring needs and management actions. The application of our results (and indeed, the model itself) to other organisms should be straightforward. The two main cautionary results are that: (1) large population sizes may mask serious long-term population viability concerns, and (2) genetic introgression of potentially maladaptive genotypes occurs with frightening speed and cannot be reversed. The consequences of low levels of mean genetic introgression persisting in populations are not known, and may in fact have little long-term population fitness impact; however, until we have empirical evidence on this point we should strive to maintain introgression of non-native genes into natural populations to a minimum and use a precautionary approach in dealing with salmon escapees.

### **Management Considerations**

In a management context, the model can serve as a synthetic perspective on the potential nature and dynamics of interactions in general to help guide policy and identify areas for research focus. However, it can also be used to develop and test specific management scenarios in the particular case study.

Conservation measures used in the model identified the need for immediate action in stopping introductions of farmed fish in the breeding population of any river where there is a will to preserve a wild, self-sustaining population of Atlantic salmon. The ways to prevent interbreeding are varied, and effectively stopping interbreeding will probably require the use of combinations of these precautionary measures. The model pointed out the need to eliminate all introductions in a population to preserve it; reductions in the number of escapees and introductions will not be effective in preserving the population, but will only alter the rate of extinction. The precautionary approach to management of the wild salmon stocks requires immediate action aimed at completely stopping introductions of farmed salmon or their ability to interbreed and survive in the wild. Wherever there is a counting fence or migratory passage facility on a river, all farmed salmon should be removed. The extensive release or escape of juvenile salmon of domestic origin from hatcheries that occurs throughout the region must be stopped immediately; the model indicated that their returns as wild spawners would greatly accelerate the rate of genetic introgression and loss of the wild stock.

### **Research Recommendations**

With the incontrovertible evidence that farmed Atlantic salmon, escaped from aquaculture sites, interbreed with wild stocks of Atlantic salmon and has some reproductive success, the model has identified the potential impacts on a wild population. Large differences in the rate at which these

impacts occur under different model scenarios revealed the importance of accurately defining the extent of interbreeding and the survival of the different offspring types that include some of the domestic genome. Research is needed to validate the model and test its predictions to understand what is going on in other stock interaction scenarios. Until it is tested, the inferences of the model remain speculative. However, the difficulties and time required in doing so in a meaningful way may be extensive and they should not delay the use of a precautionary approach.

The behaviour of the model also pointed out the need to define the survivability in the wild of the strains of salmon in use or proposed for use in aquaculture because differences in fitness have the potential to greatly alter the outcome of interactions between farmed and wild fish. Research on the migratory and spawning behaviour of farmed spawners and on the factors that control maturation in escaped farmed salmon are of utmost importance in defining the rate of impact on the wild population and the extent of genetic introgression of the domestic salmon genome. Research on the survival of offspring with different levels of introgression of the domestic genome, in the first and subsequent generations, is needed to accurately predict the rate of impact on wild salmon stocks. Without some understanding of the extent of genetic introgression in the population and its impact on fitness, attempts at management of the wild stocks that have interacted with farmed fish are bound to fail, and the impacted stocks are headed for extinction. Research and monitoring on the effectiveness of applying conservation measures, such as completely stopping introductions, on the survivability of a wild stock where some genetic introgression has already occurred should be carried out in a model system to determine the resiliency of the affected population and its ability to rebound because the attained level of introgression is irreversible.

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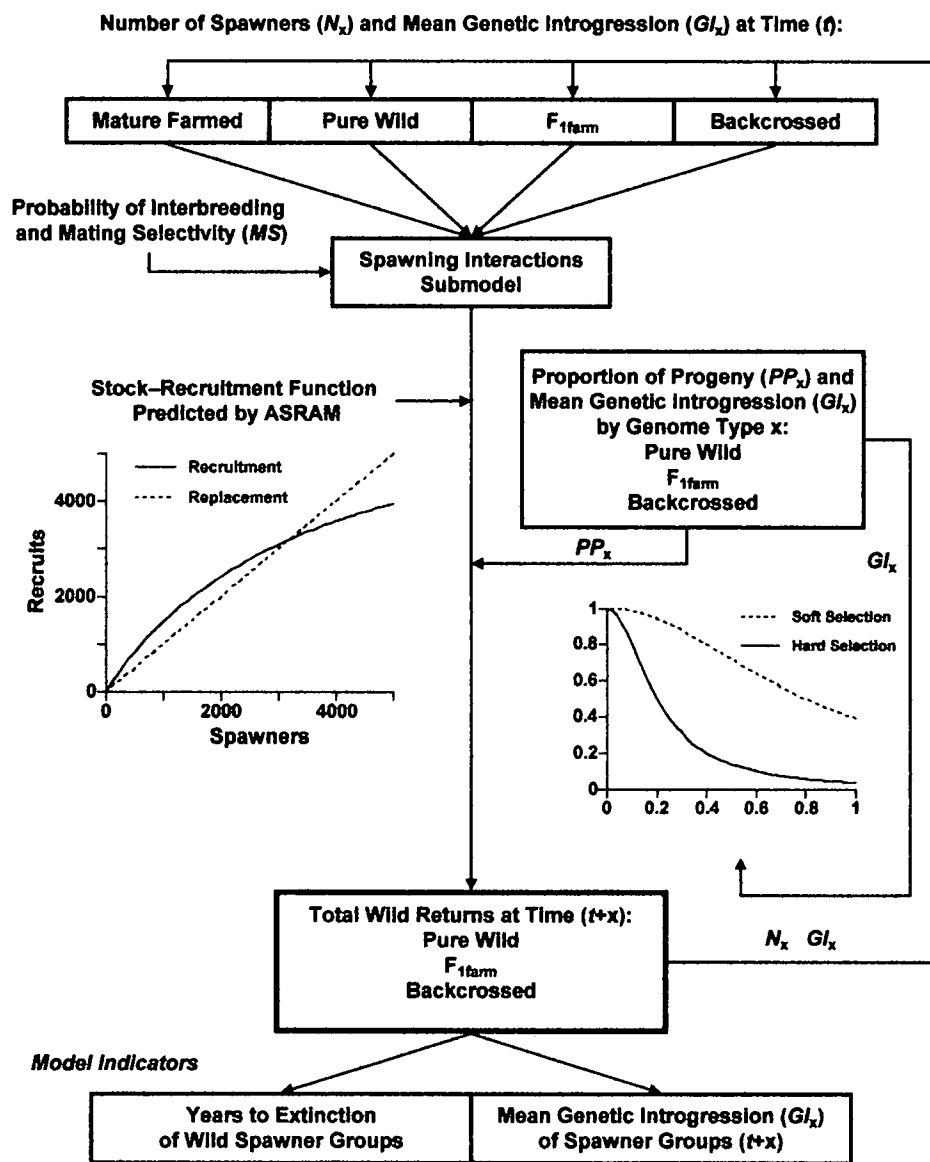


Figure 1. Conceptual representation of the interaction model for Atlantic salmon showing the four spawner groups and three genome types that are tracked, the mating component and resulting eggs, the application of proportional survival to each genome type, and the linkage of the model to the stock-recruitment relationship derived from ASRAM. Refer to Table 2 for a summary of possible matings and resulting genome types.

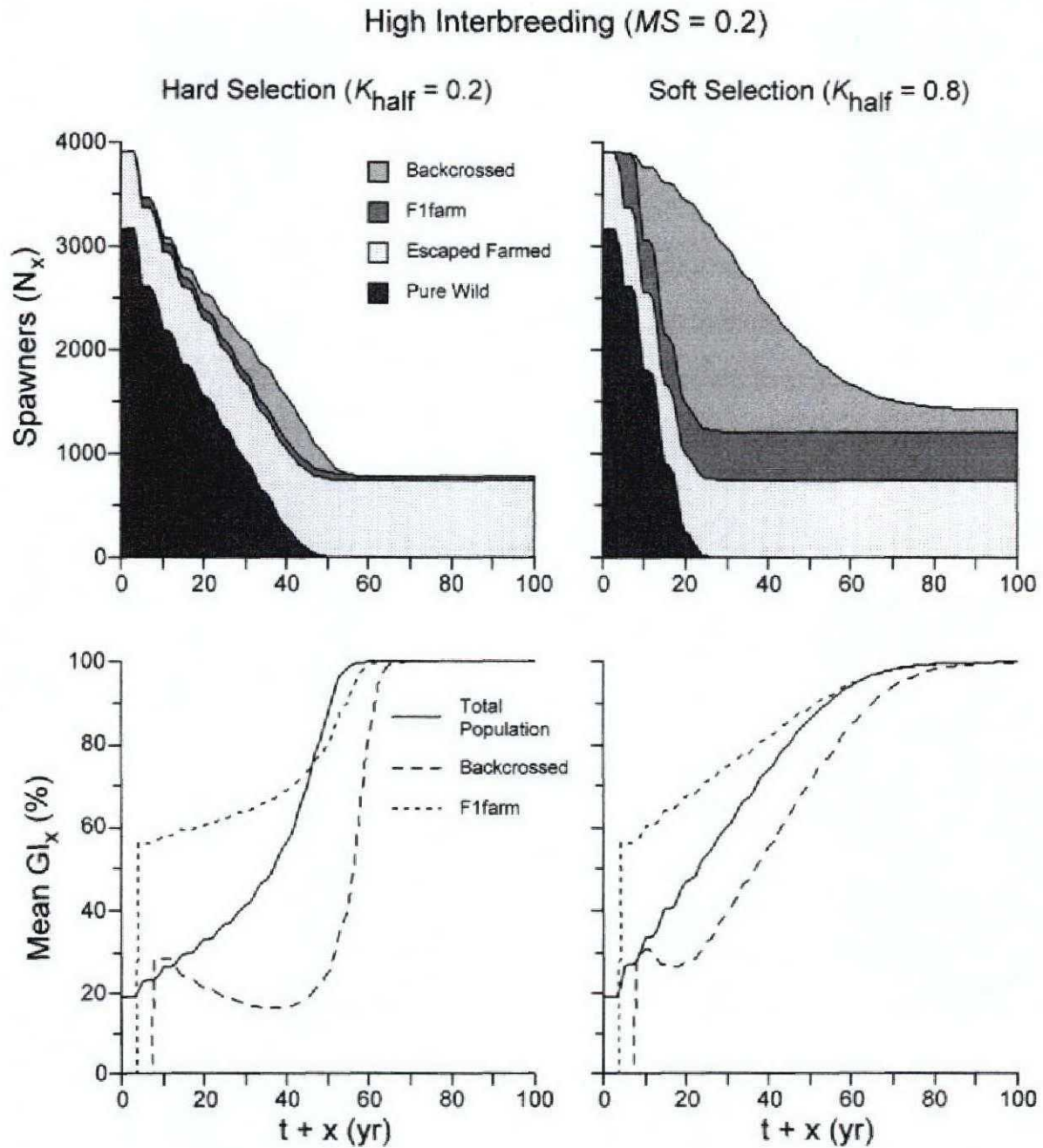


Figure 2. Model simulations of the impact of continuous introductions of escaped farmed Atlantic salmon (mean level,  $PS_{\text{farm}} = 0.2$ ) and of variation in relative survival ( $K_{\text{half}} = 0.2$  and  $0.8$ ) on the number of recruits in the four spawner groups ( $N_x$ ) and mean genetic introgression in the three genome types ( $GI_x$ ) over time in a population with a low probability of interbreeding between farmed and wild fish ( $MS = 0.2$ ).

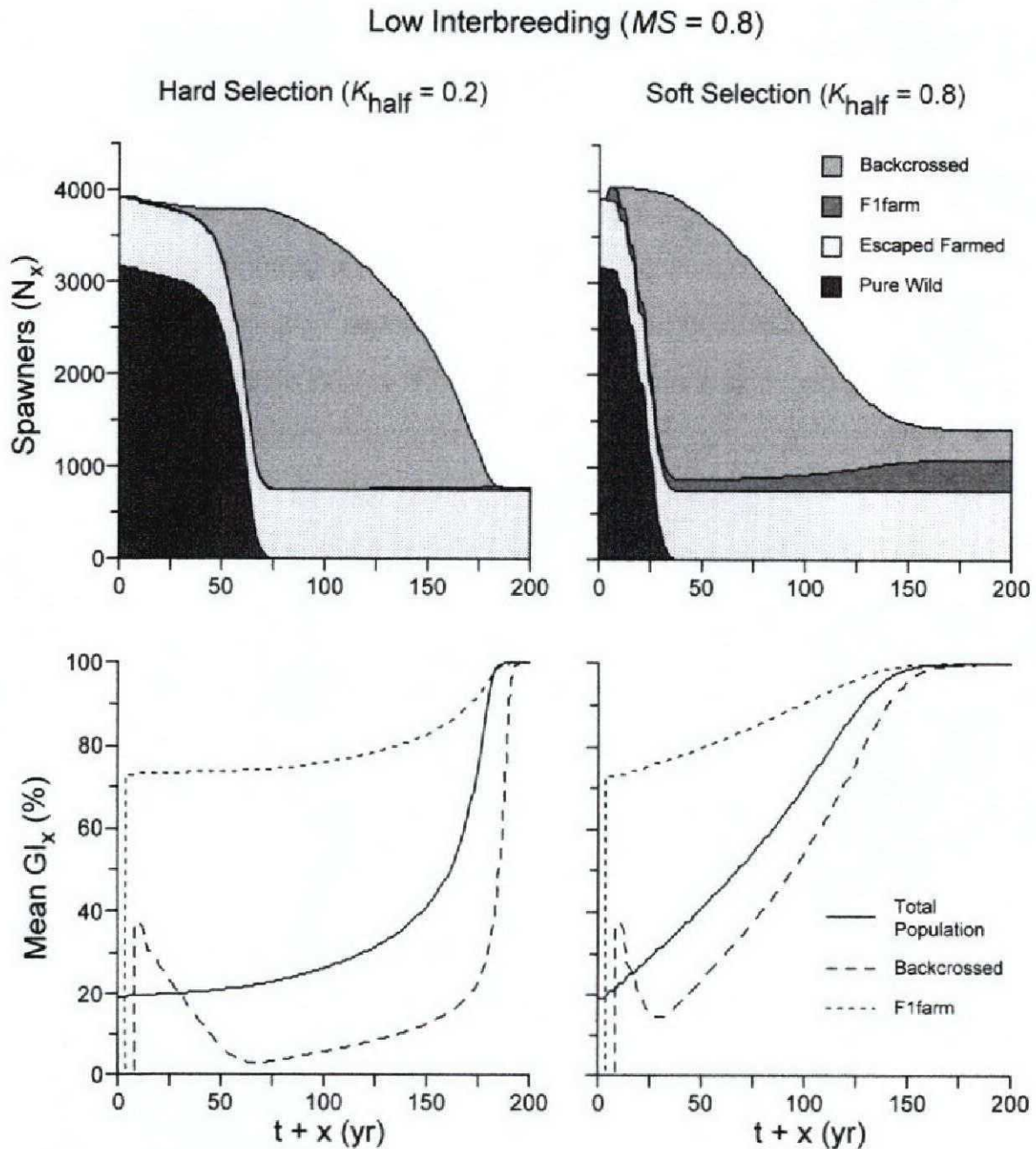


Figure 3. Model simulations of the impact of continuous introductions of escaped farmed Atlantic salmon (mean level,  $PS_{\text{farm}} = 0.2$ ) and of variation in relative survival ( $K_{\text{half}} = 0.2$  and  $0.8$ ) on the number of recruits in the four spawner groups ( $N_x$ ) and mean genetic introgression in the three genome types ( $GI_x$ ) over time in a population with a high probability of interbreeding between farmed and wild fish ( $MS = 0.8$ ).

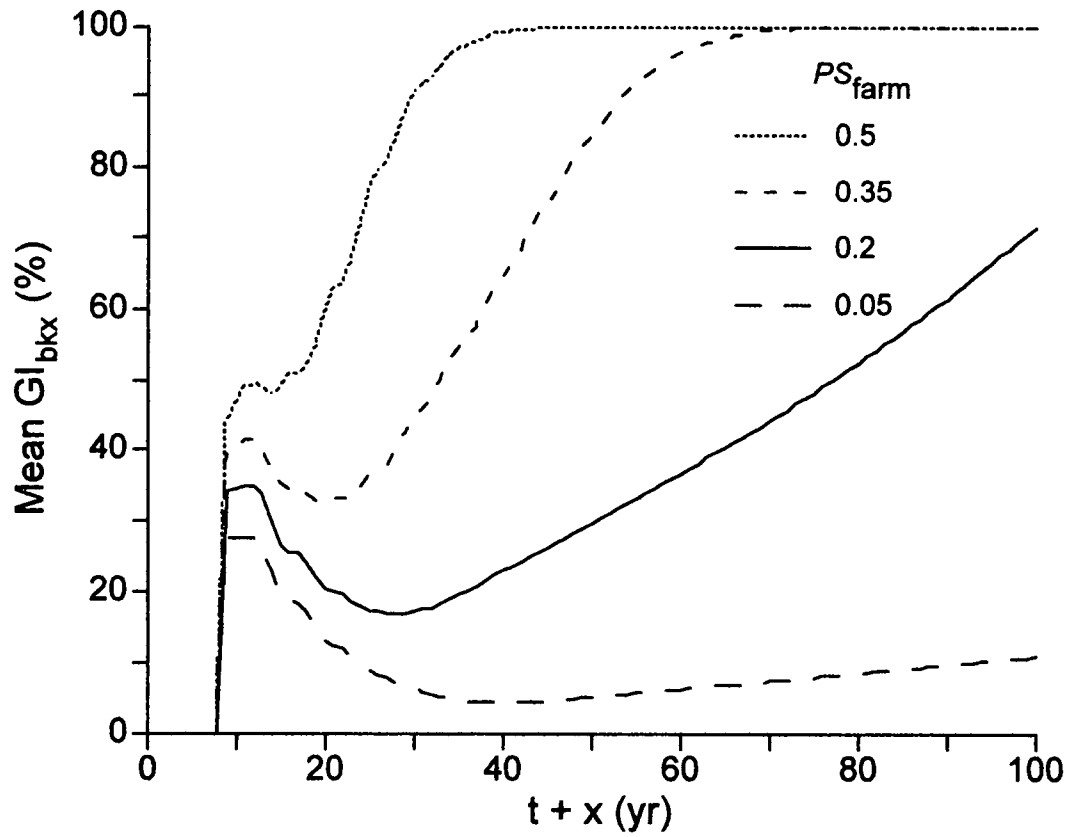


Figure 4. Model simulations of the effects of varying the magnitude of continuous introductions of escaped farmed Atlantic salmon ( $PS_{farm} = 0.05, 0.2, 0.35, \text{ and } 0.5$ ) on the mean genetic introgression in the backcrossed group ( $GI_{bkx}$ ) over time in the population of the model river ( $MS = 0.7, K_{half} = 0.8$ ).

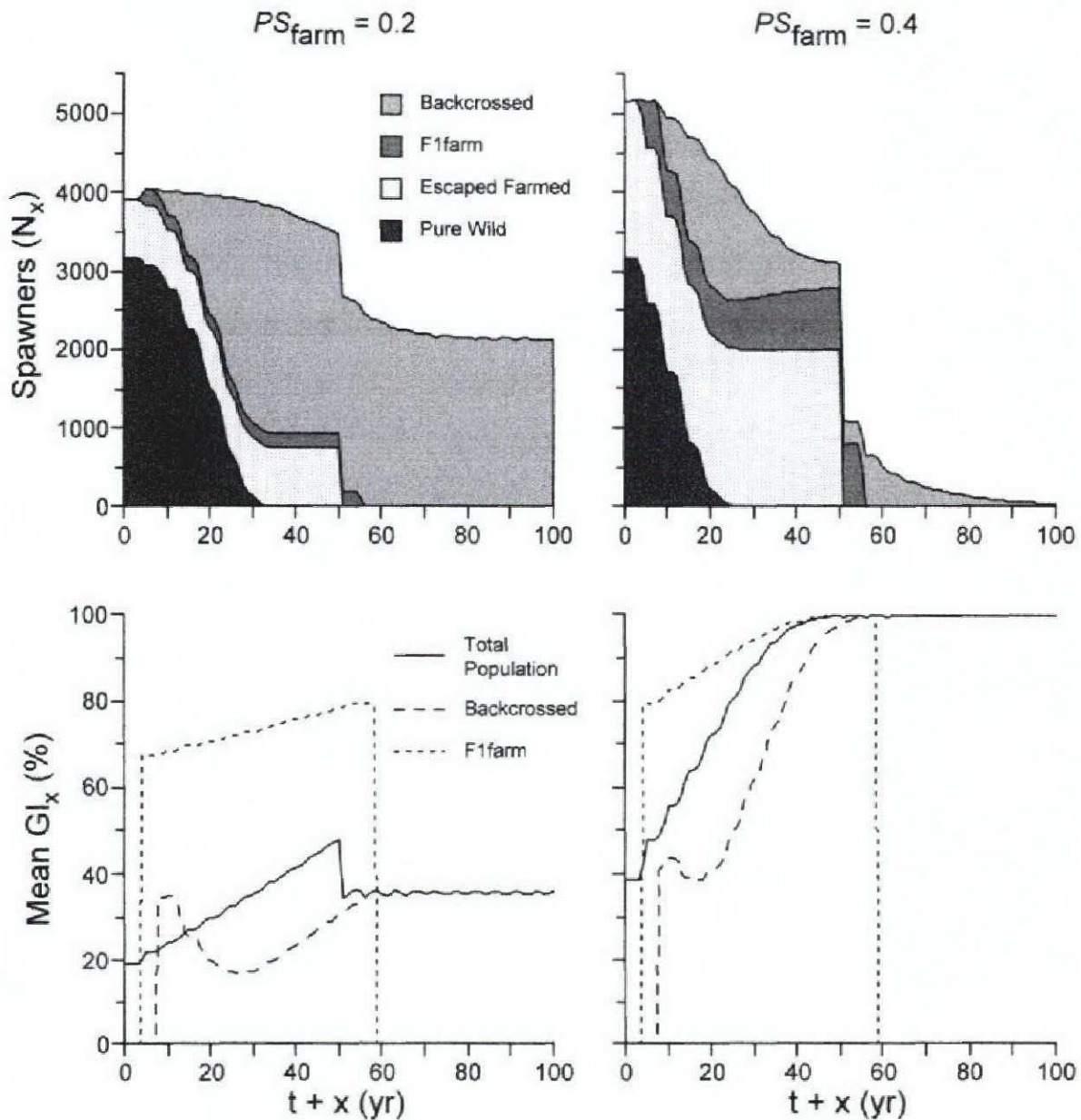
Escaped Farmed Spawners Stopped at  $t + x = 50$  yr

Figure 5. Model simulations of the impact of stopping continuous introductions of escaped farmed Atlantic salmon at two different levels (from  $PS_{farm} = 0.2$  and  $0.4$  to  $0$  at  $t+x = 50$  yr) on the number of recruits in the four spawner groups ( $N_x$ ) and mean genetic introgression in the three genome types ( $GI_x$ ) over time in the population of the model river ( $MS = 0.7$ ,  $K_{half} = 0.8$ ).

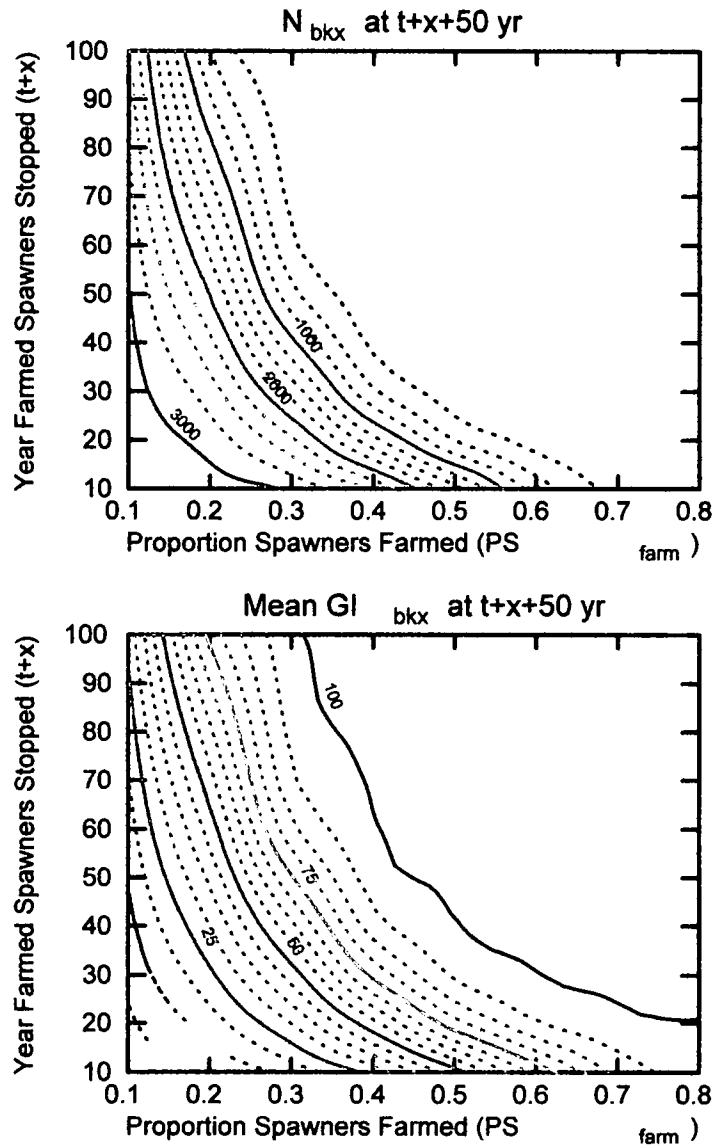


Figure 6. Results of multiple model simulations of the effects of varying the time ( $t+x = 10-100$  yr) at which continuous introductions of escaped farmed Atlantic salmon were stopped in relation to variations in the level of introduction ( $PS_{farm} = 0.1-0.8$ ) in the population of the model river ( $MS = 0.7$ ,  $K_{half} = 0.8$ ). Isopleths show the number of backcrossed spawners ( $N_{bkx}$ ) and the mean genetic introgression in the backcrossed group ( $GI_{bkx}$ ) 50 years after stopping introductions ( $t+x+50$ ).