Genetic and ecological effects of salmon farming on wild salmon: modelling from experimental results

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Cultured salmonids are released or escape into the wild in large numbers and may make up significant proportions of wild salmonid populations in fresh- and saltwater, causing considerable concern for the fitness and productivity of these populations. This paper focuses on the effects of escaped farmed Atlantic salmon (*Salmo salar*) on wild salmon. Farmed salmon have been under artificial selection for growth and other economically important traits for 30 years and are genetically different in their origin at the molecular and quantitative genetic levels. Escaped farmed salmon spawn in the wild with limited success. Their offspring outgrow those of wild origin but suffer higher mortality. Whole-river experiments in Ireland and Norway have shown that the lifetime success of farmed salmon is reduced relative to wild salmon. Based on data from these experiments, we model the future of wild salmon populations experiencing invasions of escaped farmed salmon. Simulations with a fixed intrusion rate of 20% escaped farmed salmon at spawning suggest that substantial changes take place in wild salmon populations within ten salmon generations ($\sim$40 years). Low-invasion scenarios suggest that farmed offspring are unlikely to become established in the population, whereas high-invasion scenarios suggest that populations are eventually mixtures of hybrid and farmed descendants. Recovery of the wild population is not likely under all circumstances, even after many decades without further intrusion. Managers of wild salmon will have difficulty in obtaining broodstock of the original wild population after a few generations of high intrusion. We conclude that further measures to reduce escapes of farmed salmon and their spawning in wild populations are urgently needed.

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Introduction

The Atlantic salmon (*Salmo salar*) is a highly valued species culturally and economically, generating significant revenue through both fish farming and coastal and river fisheries. The production of farmed salmon in the North Atlantic has increased dramatically since the industry began in the 1960s, reaching approximately 800 000 t in 2004 (ICES, 2005). During the same period, the total annual catch of wild Atlantic salmon in the North Atlantic declined from approximately 10 000 t in the 1960s and 1970s to 2100 t in 2005 (NASCO, 2005). Understandably, with the current 400-fold difference between farmed salmon

production and wild salmon harvests, even a small proportion of fish escaping from fish farms will make up a significant proportion of salmon in the wild. To illustrate this, an estimated 490 000 farmed salmon escaped from one Norwegian marine fish farm during a storm in August 2005. Their total weight (1300 t) exceeded the wild salmon harvest in coastal and river fisheries in Norway that year (Statistics Norway, 2006).

Concerns that escaped farmed salmon might affect wild populations of salmon were first raised in the late 1980s, when large numbers of escaped farmed salmon were observed in wild salmon spawning populations. Since then, the monitoring of wild salmon populations in Norway during

the spawning season has indicated that, on average, they include 11−35% escaped farmed salmon (Fiske *et al.*, 2001). In rivers located near fish farms and having small natural populations, up to 80% of the spawners in one season may be escaped farmed salmon, whereas rivers located far from farms and having strong natural populations may contain 5% or less escaped farmed salmon (Fiske *et al.*, 2006). The results of monitoring studies (Webb and Youngson, 1992; Crozier, 1998; ICES, 2000; Fiske *et al.*, 2001) indicate that escaped farmed salmon make up a larger proportion of catches and spawning stocks in Norway than in other countries, but escaped farmed salmon also occur, occasionally in large proportions, in Scotland, Ireland, Iceland, eastern Canada, and the US (Gudjonsson, 1991; Webb *et al.*, 1991; Carr *et al.*, 1997; Clifford *et al.*, 1998a; Butler *et al.*, 2005). In the North Atlantic, 20−40% of the salmon caught during experimental fishing in the open ocean north of the Faroe Islands during the mid-1990s were of farmed origin (Hansen *et al.*, 1999).

This paper focuses on information generated by research conducted since the major international symposium on the interactions between aquaculture and wild salmon convened by NASCO and ICES in 1997 (Hutchinson, 1997). There has been significant progress in two main areas relative to genetic and ecological impacts of farming:

(i) Standard life cycle experiments, studying farmed and wild salmon and their crosses in natural environments in Ireland and Norway, have been completed (McGinnity *et al.*, 1997; Fleming *et al.*, 2000; McGinnity *et al.*, 2003).

(ii) Molecular genetic information on wild and farmed salmon has increased (e.g. Norris *et al.*, 1999; Skaala *et al.*, 2004; Verspoor *et al.*, 2005; Roberge *et al.*, 2006), together with refined methods to distinguish individuals and populations (Cornuet *et al.*, 1999).

Significant knowledge of the spawning of mature male parr of farmed origin and of modelling the effects of gene flow has also been generated.

The life cycle experiments carried out in Ireland studied first and second-generation hybrids between wild and farmed salmon in the freshwater and marine life history phases. Three cohorts (hatched in 1993, 1994, and 1998) of Atlantic salmon were released above a fish trap in the Burrishoole system in western Ireland. Multiple families of the following seven groups were studied: native wild (all cohorts), Norwegian farmed (all cohorts), F_1 hybrid wild × farm (male and female reciprocal groups, 1993−1994 cohorts), BC_1 backcrosses to wild (1998 cohort), BC_1 backcross to farm (1998 cohort), and F_2 hybrid wild × farm (1998 cohort). As the aim of the experiment was to look at genetic differences, without the confusion of behavioural differences, eggs and milt were stripped from mature adults and artificially fertilized; group identification was determined by DNA profiling (see McGinnity *et al.* (2003) for details about the experiment).

Another life cycle experiment was undertaken in the Imsa River in southwestern Norway to quantify lifetime success (adult to adult) and behavioural−ecological interactions resulting from farmed salmon invading a native population (Fleming *et al.*, 2000). The fish were sexually mature and had been selected to ensure that native wild and farmed salmon were homozygous for different gene variants (alleles). Releases were made in autumn 1993 above a two-way fish trap, where the population could be counted at the smolt and returning adult stages (Fleming *et al.*, 2000). Parallel with the release experiment, farmed and wild salmon were introduced into a semi-natural spawning arena where their breeding performance could be monitored around the clock by direct observation and video (Fleming *et al.*, 1996).

Two recent reviews have highlighted the potential for adverse effects of aquaculture on wild salmon populations. Naylor *et al.* (2005) reported on the ecological, genetic, and socio-economic effects of escaped farmed salmon in the Atlantic and Pacific Oceans, and concluded that risks to wild populations, ecosystems, and society were high where salmon were farmed in their native range, when large numbers of salmon were farmed near small natural populations, and when exotic pathogens were introduced with farmed fish. Ferguson *et al.* (in press) focused on the genetic effects of farmed Atlantic salmon on wild salmon, and concluded that escaped farmed salmon have both indirect and direct genetic effects on wild populations, resulting in a loss of fitness (reduced recruitment) in wild populations, which are cumulative over generations in the event of continued escapes. Both reviews provided recommendations for a more sustainable coexistence of fish farming and wild salmon populations.

The goal of this study was to collate experimental data from Ireland and Norway in a way that could be used to model future scenarios for wild populations. In our basic model, we asked, (i) what is the fate of wild salmon in a river having 20% farmed immigrants during spawning for ten salmon generations? In successive modifications of this simulation, we asked, (ii) what is the effect if escapes are episodic and/or wild population sizes vary; (iii) how does the outcome differ between high-impacted and low-impacted populations; (iv) how does fitness variation among the offspring of farmed salmon in nature affect the outcome; and (v) will high-impacted populations recover if intrusions stop? We discuss our findings in the light of other biological knowledge of wild and cultured fish.

Rationale

The risks to wild salmon populations posed by escaped farmed fish can be evaluated by considering a list of biological questions of relevance to ecological, genetic, and epidemiological issues (Naylor *et al.*, 2005). In this paper, we present a quantitative risk analysis of genetic issues

and demonstrate how ecological variation affected them. It is based on published information on the proportion of escaped farmed salmon in spawning populations, their spawning success, and the survival of their offspring. This information is well-suited for modelling, but the available data have not yet been used for this purpose to any great extent. Using a broad range of possible scenarios, Hutchings (1991) modelled the threat to wild populations experiencing various intrusion rates of escaped farmed salmon and small or large fitness differences among the offspring. In our analysis, fitness is presented by life history stage in a fitness component analysis (Hedrick, 1983), and the range of scenarios narrowed, based on the recent experimental data reviewed below.

Fitness components of escaped farmed salmon and their offspring

Spawning success

Experiments in outdoor spawning arenas designed to simulate natural breeding conditions show that escaped farmed salmon typically have lower spawning success than wild salmon (Fleming *et al.*, 1996, 1997, 2000; Weir *et al.*, 2004). When farmed salmon are kept in a fish farm until just before spawning, their spawning success is much reduced relative to wild salmon. Farmed males attain only a small percentage of the spawning success of wild males, whereas farmed females may achieve approximately one-third the success of wild females (Table 1). Even when the fish have been in culture for only half a generation, as in sea ranching, the spawning success of males may be halved relative to that of wild fish. Sea-ranched females, on the other hand, seem not to experience reduced spawning success. As the sea-ranched fish studied by Fleming *et al.* (1997) were offspring of native fish, it may be expected that they represent an overestimate of the spawning success of farmed fish escaping as smolts.

The results from spawning arenas are supported by some observations in nature. Results from the experimental release of farmed fish in the Imsa indicated that they had 19% of the reproductive success (i.e. breeding and early survival) of native fish (Fleming *et al.*, 2000). Analyses of pigment variation in the eggs and early embryos, carried over from the differently pigmented farmed and wild females, suggested a mean farmed female spawning success of 0.82 relative to wild females in six Norwegian rivers (Lura, 1995). Lura (1995) suggested that the spawning success of escaped farmed females was density-dependent because their contribution of eyed eggs/embryos, relative to their proportion among the spawners, was lower in rivers and years with a high density of spawners. High frequencies of farmed female offspring in the Vosso River when few wild females were present support this finding (Sægrov *et al.*, 1997). For males, density dependence was demonstrated in a study of sea-ranched vs. wild males in which

Table 1. Spawning success of cultured and wild Atlantic salmon in natural breeding environments. (a) Relative success of anadromous spawners (mean value with range in parentheses) is estimated as the number of live embryos at the eyed-egg stage, compared with a wild spawning success of 1. (b) Proportional success of mature male parr is given as the percentage of eggs fathered by fish type in competition with anadromous males, assuming equal representation of male parr type.

(a) Anadromous individuals

Fish type	Relative success	Reference
Sea-ranched male	0.51 (0.29−0.71)	Fleming *et al.* (1997)
Sea-ranched female	0.91 (0.82−1.00)	Lura (1995); Fleming *et al.* (1997)
Farmed male	0.13 (0.01−0.24)	Fleming *et al.* (1996, 2000)
Farmed female	0.44 (0.20−0.82)	Lura (1995); Fleming *et al.* (1996, 2000)

(b) Male parr

Fish type	Proportional success	Reference
Wild × wild	4.5 (3.0−6.0)	Garant *et al.* (2003); Weir *et al.* (2005)
Wild × farmed	10.5 (8.0−13.0)	Garant *et al.* (2003); Weir *et al.* (2005)
Farmed × farmed	8.5 (4.0−13.0)	Garant *et al.* (2003); Weir *et al.* (2005)

the relative success of the former varied from 0.29 to 0.71 from high- to low-density arenas (Fleming *et al.*, 1997). Farmed males escaping late in life, however, showed inappropriate spawning behaviour and poor spawning success even in the absence of wild males (Fleming *et al.*, 1996; Weir *et al.*, 2004).

Spawning success also varies with body size. For females, fecundity increases almost linearly with body weight, and the spawning success of wild and sea-ranched females is also significantly related to body weight (Fleming, 1998). On the other hand, farmed females do not show a significant relationship between body weight and spawning success. For males, the number of embryos fathered increases exponentially with body size among wild and sea-ranched salmon, although not significantly for sea-ranched males when competing with wild males (Fleming *et al.*, 1997). Farmed males do not show a significant relationship between body weight and reproductive success (Fleming *et al.*, 1996).

Males maturing sexually at the parr stage are known to fertilize a variable proportion of eggs during the spawning of anadromous individuals (Jones and Hutchings, 2002). Experiments by Garant *et al.* (2003) and Weir *et al.*

(2005) suggest that mature male parr resulting from crosses between escaped farmed salmon, or between farmed and wild fish, may attain an individual spawning success up to four times higher than that of wild offspring (Table 1). However, the two experiments were quite similar in the total proportion of offspring fathered by parr (24% and 23%, respectively). The spawning success of anadromous offspring of escaped farmed salmon has not been studied in detail. Artificial crosses suggest that F_2 hybrids may suffer high egg mortality, compared with all other types of second-generation offspring (McGinnity *et al.*, 2003).

Survival

Wild × wild crosses had the highest lifetime survival of all offspring groups, both in the Imsa and Burrishoole experiments (Fleming *et al.*, 2000; McGinnity *et al.*, 2003). However, when partitioning the survival into several life stages, the various short-term survival rates could be higher for some of the other groups (Table 2). From deductions of the comparison between age 0+ fish electrofished in the Imsa and breeding success in spawning arenas, it appears that, from eyed eggs to the first autumn, farm × farm crosses could have up to 43% higher survival rates than wild × wild crosses, but on average survived 12% less (Table 2). From the first autumn to the smolt stage, several groups showed higher survival than wild × wild crosses in Burrishoole. In particular, F_2 hybrids and backcrosses to wild and farmed fish survived far better than wild fish, if it was assumed that parr displaced downstream do not survive (McGinnity *et al.*, 2003). This is probably a realistic assumption for populations that are fully recruited and for populations where downstream displacement is equivalent

to entering the sea before smolting, or a combination of both scenarios.

Survival in the ocean varied little among groups in the Imsa experiment, bearing in mind that numbers are small, but showed considerable variation in the Burrishoole experiments (Table 2). Farm × farm crosses and backcrosses to farmed fish showed very poor survival relative to wild fish in the Burrishoole. Additional experiments in the Imsa between 1996 and 1998 also showed significantly lower smolt-to-adult survival of farm × farm crosses than wild × wild crosses (IAF, unpublished). In these experiments based on releases of cultured smolts in the Imsa, relative survival of farm × farm crosses was on average 37% of wild × wild crosses. Wild × farm crosses, on the other hand, did not show significant differences from wild × wild crosses.

Growth rate and body size

Individual growth rate was higher among farm × farm and wild × farm crosses than wild × wild crosses in both the Imsa and Burrishoole experiments. In the Imsa, pure farmed and hybrid offspring were significantly larger than pure wild offspring at the end of the first growing season (age 0+; Fleming *et al.*, 2000). In the Burrishoole system, farmed 0+ parr were largest in size, wild parr smallest, and hybrids intermediate (McGinnity *et al.*, 1997).

On return as sexually mature fish, body size did not differ significantly among groups in the Imsa experiment (Fleming *et al.*, 2000), but the numbers were small. Additional smolt releases between 1996 and 1998, showed that crosses involving farmed fish were larger than wild × wild crosses upon return from the sea (IAF, unpublished). In the Burrishoole system, returning farmed salmon were significantly larger than returning wild salmon. As a consequence, fecundity was

Table 2. Survival of various crosses between farmed and wild Atlantic salmon in natural environments, relative to a wild × wild survival of one. Experimental data (mean value with range in parentheses) are from the Imsa River and the Burrishoole system. For backcross to wild, backcross to farmed, and second-generation hybrids, the first and second relative survival values refer to different assumptions about the fate of displaced parr (McGinnity *et al.*, 2003). The first value assumes that displaced parr have the same survival as the same group remaining in the experimental river (i.e. river parr density below carrying capacity); the second value assumes that displaced parr do not survive (i.e. river parr density is at carrying capacity).

Fish type	Eyed eggs to 0+ in autumn	0+ in autumn to smolt	Smolt to adult	Reference
Wild × wild	1	1	1	
Farmed × wild; wild × farmed	0.67 (0.63−0.71)	0.92 (0.54−1.13)	0.85 (0.43−1.21)	McGinnity (1997); McGinnity *et al.* (2003); Fleming *et al.* (2000)
Farmed × farmed	0.88 (0.49−1.43)	1.06 (0.61−1.53)	0.33 (0.03−0.83[*])	McGinnity (1997); McGinnity *et al.* (2003); Fleming *et al.* (2000)
Backcross to wild	0.81, 0.80	1.10, 1.43	1.03	McGinnity (1997); McGinnity *et al.* (2003)
Backcross to farmed	0.71, 0.77	1.12, 2.07	0.32	McGinnity (1997); McGinnity *et al.* (2003)
Second-generation hybrid	0.75, 0.81	1.30, 2.30	NA	McGinnity (1997); McGinnity *et al.* (2003)

NA, not analysed.

[*]$n = 1$.

also considerably higher in returning farmed salmon than in returning wild salmon (McGinnity *et al.*, 2003).

Life history

Several life history traits differed among the experimental groups, with considerable variability between the Imsa and Burrishoole experiments (Table 3). The rate of sexual maturation among male parr was higher among wild offspring than among farmed and hybrid offspring in both experiments, although estimated at different ages (age 0+ in the Imsa and age 1+ in the Burrishoole). Smolt age was lower among farmed and hybrid offspring in the Imsa, but did not differ among groups in the Burrishoole (Table 3).

On the other hand, sea age at return did not differ among Imsa groups, but in the Burrishoole was considerably higher among crosses involving farmed salmon than for wild salmon (Table 3). Farmed salmon largely matured as two sea-winter fish, whereas wild Burrishoole salmon matured as one sea-winter fish.

Combining the variation in smolt age and sea age at return, the mean age at sexual maturity was lower for farmed and hybrid salmon relative to wild salmon in the Imsa, whereas the opposite was true in the Burrishoole.

Model

In modelling the fate of wild salmon populations following intrusions of escaped farmed salmon, we focused on the effects of interbreeding and differential survival. The results are presented as proportional contributions of different

categories of fish to the population, and how these proportions change through time. We ignored spatial effects, such as variation between rivers, and made a deterministic model using the combined information from the experiments summarized above. Although the sex ratio of anadromous adults on the spawning grounds can vary widely among wild Atlantic salmon populations (20−>90% female; Fleming, 1998), as well as among escaped farmed salmon (26−50% female; Fiske *et al.*, 2001), an equal sex ratio for all categories was assumed for simplicity.

As input, we used data on the occurrence of escaped farmed salmon in spawning populations in Norway (Fiske *et al.*, 2001), which averages an influx of $p_f = 20\%$ escaped farm fish every breeding season. Half of these fish were assumed to have escaped early in their marine life and the rest late in marine life (Lura and Økland, 1994). Late-escaping females were assumed to have a larger body size and on average 40% more eggs (P. Fiske, pers. comm.) than the other female categories. Escapes of juveniles from hatcheries into rivers were ignored because of the lack of reliable estimates of number. Their inclusion, however, would only reinforce the changes implied by the models (Clifford *et al.*, 1998b). A population vector was constructed using the different categories of anadromous spawners (wild, farm early escape, farm late escape), and assuming that 23−24% of the eggs are fertilized by mature parr (Garant *et al.*, 2003; Weir *et al.*, 2005).

A spawning success vector was constructed for females and males, using the estimates obtained from Table 1. We estimated the contribution of a particular cross by making an egg pool from the proportions of female spawners

Table 3. Life history of various crosses between farmed and wild Atlantic salmon in the Imsa and Burrishoole experiments.

Fish type	Proportion of mature parr	Smolt age (years)	Sea age (years)	River	Reference
Wild × wild	0.18[*]	1.68	1.22	Imsa	Fleming *et al.* (2000)
Farmed × wild; wild × farmed	0.13[*]	1.34	1.38	Imsa	Fleming *et al.* (2000)
Farmed × farmed	0.14[*]	1.07	1‡	Imsa	Fleming *et al.* (2000)
Wild × wild	0.18−0.51†	2	1.02−1.05	Burrishoole	McGinnity (1997); McGinnity *et al.* (2003)
Farmed × wild; wild × farmed	0.14−0.32†	2	1.63−1.67	Burrishoole	McGinnity (1997); McGinnity *et al.* (2003)
Farmed × farmed	0.04−0.12†	2	1.86−2.00	Burrishoole	McGinnity (1997); McGinnity *et al.* (2003)
Backcross to wild	0.14†	2	1.05	Burrishoole	McGinnity (1997); McGinnity *et al.* (2003)
Backcross to farmed	0.05†	2	1.24	Burrishoole	McGinnity (1997); McGinnity *et al.* (2003)
Second-generation hybrid	0.15†	2	NA	Burrishoole	McGinnity *et al.* (2003)

NA, not analysed.
[*]Proportion of mature individuals among males at age 0+.
†Proportion of mature individuals among migrating parr at age 1+.
‡$n = 1$.

multiplied by their fecundity and spawning success, followed by fertilization by different categories of males with their respective proportion and spawning success. (F_2 hybrids in the Burrishoole experienced additional egg mortality not explained by female or male gamete quality; McGinnity *et al.*, 2003). From these calculations, the different categories of eyed eggs were derived. For most of these categories, their spawning success on return as anadromous fish is unknown and is assumed to be equal to that of wild fish.

A survival vector was constructed for the different categories of offspring, using the data partitioned into early survival (eyed eggs to first autumn), late parr survival (first autumn to smolt), and marine survival (smolt to adult) shown in Table 2. Because proportional contributions were used, we implicitly worked from the same point on the stock-recruitment curve for all years, i.e. the absolute population size was the same for all years.

Throughout the model, we used the following notation:

W	Wild
FE	Farm early escape (post-smolt)
FL	Farm late escape (sub-adult)
WW	Wild female × wild male
WF	Wild female × farm male
FW	Farm female × wild male
FF	Farm × farm
H	Hybrid (of FW or WF origin)
FeralF	Wild farmed or feral fish (of FF origin, but lived all their life in the wild)

Different forms of the model were examined, building from a basic simulation by adding increasing complexity or realism. The basic scenario examined the outcome of a fixed proportion of escaped farmed salmon each year and focused solely on anadromous adults, ignoring contributions by mature male parr. Complexity (realism) was added by: (i) varying the intrusion rates annually; (ii) varying spawning success; (iii) including contributions by mature male parr; and (iv) varying survival rates during different life stages. The final scenario addressed the potential for recovery of highly-impacted populations if intrusions of escaped farmed fish ceased.

Results

Basic simulation

In our basic simulation, we assumed a fixed proportion of 20% escaped farmed salmon in the spawning population, that half of these escaped during their first year at sea, and that late-escaping farmed females have 40% higher fecundity than wild females. Using the population vector [Wild, Hybrid, FeralF, FarmEarly, FarmLate], we extracted from Table 1 a female spawning success vector of [1, *1*, *1*, 0.91, 0.44] and a male spawning success vector of [1, *1*, *1*, 0.51, 0.13], assuming that no mature male parr participated

in spawning. Italicized figures within vectors are a best guess in the absence of experimental data.

From Table 2, we extracted a set of survival vectors [WW, WF/FW, FeralF, BC-W, BC-F, F_2] where BC-W and BC-F are backcrosses to wild and farmed fish, respectively, and F_2 are second-generation hybrids. We used the vectors [1, 0.67, 0.88, 0.8, 0.71, 0.75] for survival from eyed egg to the end of the first summer, [1, 0.92, 1.06, 1.10, 1.12, 1.30] for survival from first summer to smolt, and [1, 0.85, 0.33, 1.03, 0.32, *0.8*] for survival from smolt to adult (Table 2). The numbers in the vectors represent relative survival rates for each category of fish, averaged over the experiments listed in Table 2. For three categories, BC-W, BC-F, and F_2, we used a conservative estimate of relative survival between the eyed egg and smolt stages, i.e. we assumed that displaced parr had the same survival rate as those remaining above the fish trap in the Burrishoole system (McGinnity *et al.*, 2003). No data exist for the sea survival of second-generation hybrids, which was set at 0.8.

Simulations over ten generations, approximately 40 years, showed a steady decline in the proportion of wild fish in the population (W), a steady increase in the proportion of hybrids (H), and a small proportion of wild farmed fish (FeralF; Figure 1). In these simulations, half of the backcrosses of hybrids to wild fish were allocated to the W group and half to the H group to reduce the number of categories. Similarly, half of the backcrosses to farmed offspring were allocated to the FeralF group and the other half to H. Second-generation hybrids were allocated entirely to the H group. As a result, the H group eventually consists of a diverse set of first- and late-generation hybrids, as well as half of the various
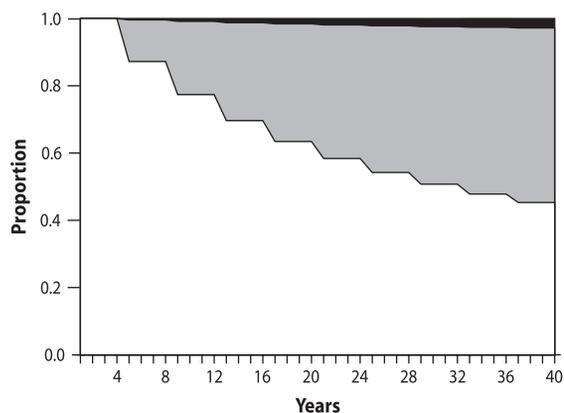

Figure 1. Development of a salmon population receiving 20% escaped farmed salmon during ten generations (approximately 40 years). The input data are average values on spawning success and survival from Tables 1 and 2. Mature parr are not included. The output is the composition of the andromous spawning population before the new influx of escaped farmed salmon, so that no change is evident during the first generation. The sectors in the figure represent the proportion of wild fish (□), hybrids (▨), and feral farmed fish (■). See text for categorization of wild fish, hybrids, and feral fish.

backcrosses to wild and farmed fish. Furthermore, the W and FeralF groups include a proportion of the backcrosses, in addition to fish of entirely wild and farmed pedigrees, respectively.

Effect of varying intrusion rates

If escapes occur episodically, large changes in the population will follow a large intrusion of escaped farmed salmon. In periods with no intrusions, a slow increase in the proportion of wild fish will occur until the next intrusion. Time-series from two Norwegian rivers illustrate this point (Figure 2). Simulations for the Stjørdalselva River in the middle of Norway, where the proportion of escaped farmed
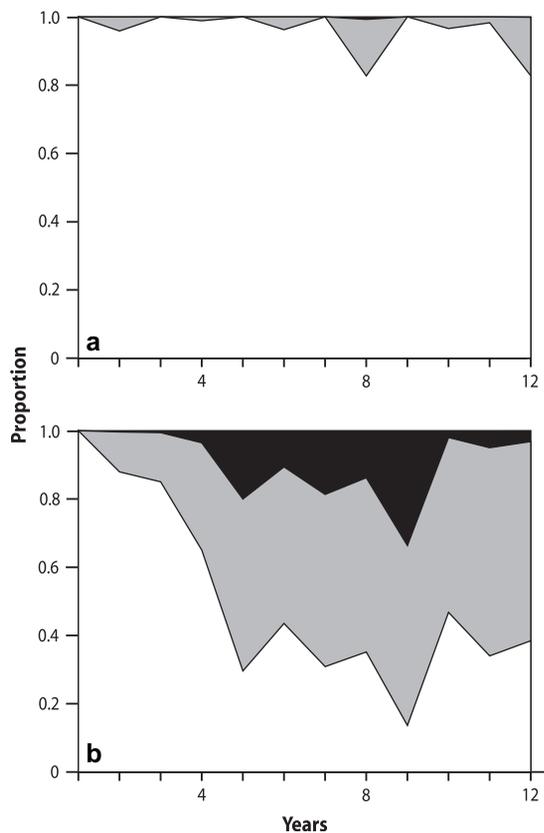

Figure 2. Varying intrusion rates over time in rivers with contrasting farmed salmon intrusions. (a) data on the proportion of escaped farmed salmon in the spawning populations from the Stjørdalselva River, and (b) the Vosso River for the years 1989–2000, from Fiske *et al.* (2001). In years with no data or a small number of fish, the proportion of escaped farmed salmon was set at zero (italicized), giving the intrusion vectors [*0*, 0.07, *0*, 0.02, *0*, *0*, *0*, 0.25, *0*, *0*, 0.03, 0.03] for the Stjørdalselva River and [*0*, 0.19, 0.23, 0.46, 0.75, 0.61, 0.71, 0.59, 0.65, *0*, *0*, *0*] for the Vosso River. Mature parr are not included. Spawning success and survival vectors are as in Figure 1, but output shifted one generation to the left (i.e. not showing four years with no change). The sectors in the figure represent the proportion of wild fish (□), hybrids (▨), and feral farmed fish (■).

salmon between 1989 and 2000 varied between 0% and 7%, but was as high as 25% in one year (Fiske *et al.*, 2001), indicate that such a population would continue to be dominated by wild fish (Figure 2a). There would also be a small proportion of hybrids and no FeralF offspring. An occasional decline in the proportion of wild fish occurred following a high-intrusion year, with further decline four years later as a result of the spawning of their offspring.

In contrast, Figure 2b shows simulations for the Vosso River in western Norway in which the proportion of escaped farmed salmon varied between 19% and 75% during eight consecutive years in the 1990s. In this population, a decline in the proportion of wild fish from more than 80% to about 40% occurred during only eight years of high rates of intrusion. A slight increase in the wild proportion appeared to occur during the next three years, when no intrusions of farmed salmon were included in the model. (In reality, most of the spawners during those three years were escaped farmed salmon; DN, 2005).

If the proportion of escaped farmed salmon in the population varies from year to year according to a beta distribution with a given mean value, simulating stochastic variation, the rate of decline in the proportion of wild fish will be slightly more rapid than if the proportion of escapes is fixed at the same mean level. This is because there will be a disproportionately high impact on the composition of the population from the occasional years with intrusion rates much higher than average.

Effect of varying spawning success of escaped farmed salmon

Farmed fish may show considerable variation in spawning success (Table 1). We constructed new spawning vectors for both females and males, using figures from either the low or high range of observations. Low spawning success of farmed fish was based on a 1% relative spawning success of males escaping late and 29% success of males escaping early; the corresponding figures for females were 20% and 82% (Table 1). For spawners belonging to the WF/FW and FeralF groups, which have not been studied, we also reduced the spawning success in this simulation to levels resembling early-escaping farmed fish (for FeralF) or the midpoint between this level and 100% (for WF/FW).

The results suggest that the low spawning success of escaped farmed salmon may significantly increase the wild proportion after ten generations (Figure 3), whereas values from the high range of observations have relatively little effect on the proportion of wild fish in the population, but increase the proportion of FeralF fish.

Sexually mature parr and ecological realism

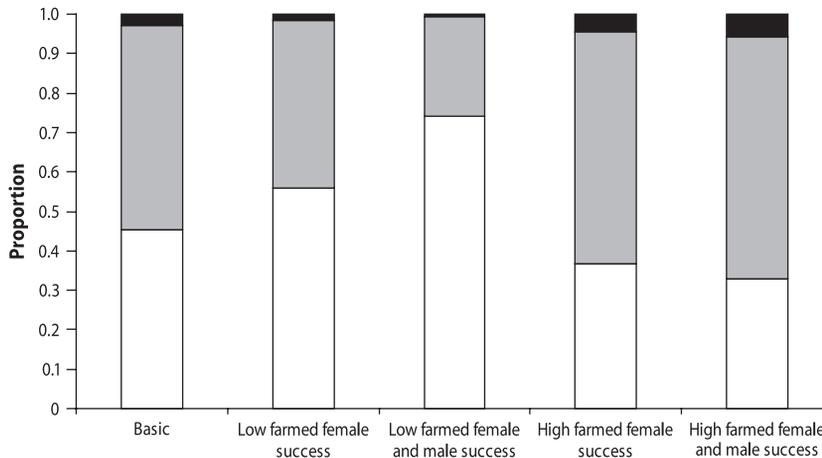In the Imsa experiment, 18% of the wild age 0+ males were sexually mature (Table 3), but this proportion was

Figure 3. Varying relative spawning success of farmed escaped salmon from low to high. The proportion of wild fish (□), hybrids (▨), and feralF fish (■) after ten generations of intrusions is shown for the basic simulation (cf. Figure 1), and for farmed females, or farmed males and females, having either low or high spawning success according to the observations presented in Table 1.

slightly lower for hybrid males (13%) and FeralF males (14%). Using these proportions, a total male parr contribution of 23.5%, and a relative parr success ratio of [4.5, 10.5, 8.5] for the three groups (Garant *et al.*, 2003; Weir *et al.*, 2005), mature male parr increased the rate of the decline in the proportional representation of wild fish in the population (Figure 4), the biggest influence being early in each new generation of farmed influx. The resulting proportion of wild fish after 40 years was 37% with spawning of sexually mature parr, compared with 45% when ignoring mature parr.

We did not carry out simulations based on the rates of parr maturity found in the Burrishoole experiments (Table 3) because they were estimated for older parr (age 1+), whose relative proportions were not included in the model. In nature, however, there is a large variation in the age and rate of male parr maturity and relative success (Hutchings and Jones,

1998; Jones and Hutchings, 2002). This makes spawning by mature males a potentially important route for gene flow from farmed to wild salmon (Garant *et al.*, 2003).

Effect of varying fitness components during different life stages

The outcome of several simulations is compared in Figure 5, which further explores variation in relative survival rates. In these simulations, all experimental groups were given either low or high survival relative to pure wild fish during a particular life stage, whereas mean values were used for the other life stages. The effect on the proportional representation of the population was compared after ten generations of intrusions. The largest effect on the composition of the population is caused by varying the survival rates of age 0+ fish to smolts (Figure 5), variation that could be the result of whether or not the population was at carrying capacity. The former imposes a penalty on wild fish because they were over-represented among the fish that were displaced downstream in the Burrishoole experiment (McGinnity *et al.*, 2003).

The effect of different generation time between wild salmon and offspring of farmed salmon, evident in both the Imsa (generation time of FeralF salmon ∼0.8 years shorter than native salmon) and Burrishoole experiments (∼0.9 years longer), has not been modelled yet. The longer generation time of farmed salmon in the Burrishoole was associated with both higher fecundity and lower marine survival, as two-sea-winter salmon were bigger, but returned at a lower rate. When running the model with higher fecundity and lower marine survival of FeralF salmon, i.e. using Burrishoole data, as opposed to fecundity and marine survival being more similar, as in the Imsa, between wild and FeralF salmon, simulations (not shown) suggested that the two types of life histories gave similar outcomes.
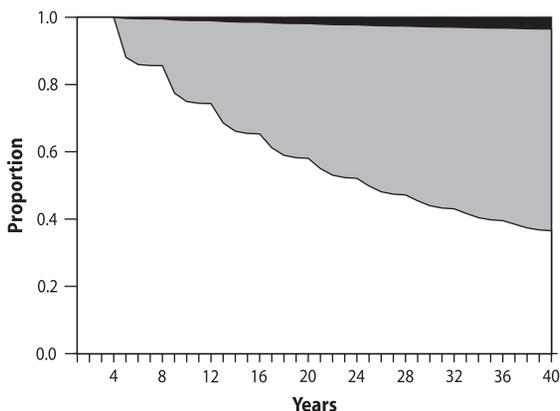

Figure 4. Effect of sexually mature male parr on the proportion of wild fish (□), hybrids (▨), and feralF fish (■). Otherwise the same data as in Figure 1.
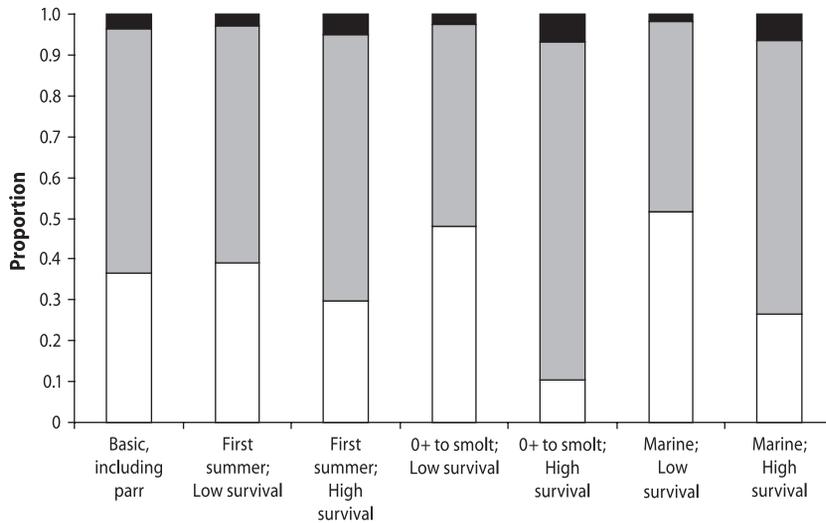
Figure 5. Varying relative survival rates of farmed offspring from low to high values during different life stages. The proportion of wild fish (□), hybrids (▨), and feralF fish (■) after ten generations of intrusions for the "basic, including parr" simulation (Figure 4), and for fish with farmed ancestry having either low or high survival according to the observations presented in Table 2.

Recovery of highly-impacted populations

An interesting question is whether or not highly-impacted populations will recover if intrusions of escaped farmed fish cease. Two simulations suggest that this question may have widely differing answers (Figure 6). If the input data used for the highly-impacted population (Figure 2b) were continued for 100 years without any further intrusion of escaped farmed salmon, the proportion of wild fish would eventually return to 100% (Figure 6a). This situation occurs following many decades of dampened oscillations from the year-to-year variation introduced by the first decade of variable intrusion rates. Such oscillations have been noted previously when modelling allele frequency changes following immigration into populations with overlapping generations (Ryman, 1997).

However, if the input data were changed so that male parr spawning is included and FeralF and hybrid offspring return as larger, more fecund fish than wild fish, the long-term trend appeared to be one of complete dominance by hybrid fish (Figure 6b). As our model does not distinguish between second and later generation hybrids and backcrosses, the possible re-adaptation after more than 20 generations without further intrusion was not modelled. However, the simulations suggest that, after 20 generations, the population modelled in Figure 6b had a markedly different composition of farmed-wild ancestry from the population modelled in Figure 6a.

Discussion

The whole-river experiments that provide the data for our model cover one cohort of native wild and Norwegian

farmed salmon (AquaGen strain) in the Imsa River, and three cohorts of native wild and Norwegian farmed salmon (Mowi strain) in the Burrishoole. They show a common result, a higher lifetime survival of native wild fish than for all other first- and second-generation crosses. There is, however, variation in the details, both between the Imsa and Burrishoole experiments and among the cohorts within the Burrishoole. Some of this variation can be explained by Norwegian farmed salmon having a higher sea age at sexual maturity than wild Burrishoole fish. Other differences might reflect variation in the environment or experimental set-up. Rather than trying to explain the variation observed, we have used the different estimates in a model to illustrate the range of variation that might occur during interaction between escaped farmed and wild salmon.

The results of the simulations give rise to concerns for most wild populations that receive average (ca. 20%) or larger proportions of escaped farmed salmon. For scenarios involving high survival of farmed offspring (Figure 5), wild populations would be at risk at smaller proportions of escaped farmed salmon. In high-intrusion scenarios, managers of wild salmon will have difficulties in obtaining broodstock of the original wild population after a few generations. Therefore, the assumptions in the model and the experimental input data used need to be examined carefully. The Imsa and Burrishoole wild salmon populations live in similar environments and have similar life histories. They represent only a small fraction of the variation in Atlantic salmon life histories observed within the range of this species (Schaffer and Elson, 1975; Metcalfe and Thorpe, 1990; Hutchings and Jones, 1998). Therefore, the experimental data on interaction between wild and farmed salmon may not be applicable across the species' range.
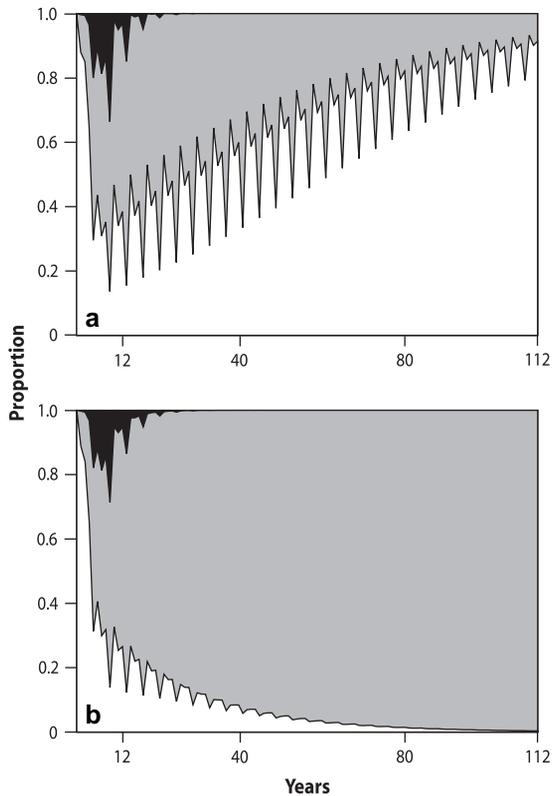
Figure 6. Long-term trends in a wild salmon population receiving farmed immigrants as in Figure 2b for the first 12 years, followed by 100 years of no further escapes. Panel (a) uses the same input data as in Figure 2b, whereas panel (b) includes mature male parr and assumes that farmed and hybrid spawners are more fecund than wild fish. The sectors in the figure represent the proportion of wild fish (□), hybrids (▨), and feral farmed fish (■).

First, we have not studied interactions between escaped farmed salmon and wild populations in North America or in the Baltic Sea, which differ genetically from populations in western Europe (Ståhl, 1987; King *et al.*, 2001). Second, we have not studied interactions using wild fish populations having a high smolt age or high sea age-at-maturity or a combination of both factors. Third, escaped farmed salmon typically spawned earlier than wild fish in the Imsa experiments, but may spawn later than wild fish in other locations and add new types of interactions (e.g. over-cutting of the redds of wild females; Lura and Sægrov, 1991). On the other hand, the experiments that provided the input data for our model used a combination of farmed strains, environments, and wild populations that represent the most common interactions between farmed and wild Atlantic salmon. Norwegian farmed strains account for a large proportion of farmed salmon production (Gjøen and Bentsen, 1997). Moreover, southwestern Norway and western Ireland are both important fish-farming areas, and escaped farmed salmon are common in both areas (Gausen and Moen, 1991; Clifford *et al.*, 1998a, b; Fiske *et al.*, 2001, 2006).

Exclusion of the effects of density-dependence and population regulation is probably the most important limitation of the current model. First, density-dependent spawning success of farmed females has been reported by Lura (1995), and of sea-ranched males by Fleming *et al.* (1997). In both cases, a higher density of wild fish reduced the spawning success of cultured fish. Second, the survival rate of the offspring is likely to be density-dependent during critical periods of their freshwater life. Stock-recruitment (SR) relationships in the Imsa River suggest that survival is density-dependent during the parr stage, whereas it is density-independent during seawater life (Jonsson *et al.*, 1998). A recent study suggests that important density-dependent mortality takes place during the first year of parr life (Einum and Nislow, 2005). In the Burrishoole experiments, McGinnity *et al.* (1997, 2003) found varying levels of survival among groups within cohorts (e.g. by a factor of two for the farmed group), depending on whether they considered juvenile fish captured migrating out of the experimental stream as survivors and occupying habitats downstream of the trap or as mortalities and thus lost to the system. Third, in the Imsa experiment there was a ca. 30% reduction in total smolt output compared with the SR-relationship, suggesting that high intrusions of farmed salmon may result in reduced population size. Reduced productivity was also found in the Burrishoole experiment, even when taking the increased fecundity of returning farmed fish into consideration (McGinnity *et al.*, 2003). In steelhead trout (*Oncorhynchus mykiss*), Chilcote (2003) found that in mixed populations of wild and hatchery fish, equal numbers of the two would produce 63% fewer recruits per spawner than one composed entirely of wild fish. Some of these effects, e.g. reduced smolt output, could be studied in our model by allowing the same number of escaped farmed fish to make up an increasing proportion of the spawners. However, a full study of density-dependence would require knowledge of how spawning success and survival rates varied with density.

A model incorporating density-dependent effects of escaped farmed fish on wild populations was developed by Tufto (2001). He used a quantitative genetic model that included immigration of maladapted individuals into wild populations, where the outcome was determined by density-dependent regulation and local stabilizing selection. One result was a reduction in total equilibrium size (carrying capacity), when immigrants deviated more than 2.8 genetic standard deviations from the local optimum and immigration was high, relative to the strength of stabilizing selection. Comparison of the selected strains of farmed Atlantic salmon and wild populations (e.g. growth rate) suggests that the above conditions are typical of those currently in many rivers (Tufto, 2001).

Another effect not examined in our model is the impact of escaped farmed salmon on genetic variability. Farmed salmon typically show lower genetic variability than wild salmon populations (Mjølnerød *et al.*, 1997; Norris *et al.*,

1999; Skaala *et al.*, 2004). One-way gene flow from farmed salmon to wild populations eventually results in the effective population size, and consequently in the rate of loss of genetic variation, being determined by the effective population size of the farmed salmon (Tufto and Hindar, 2003). The effective population size of farmed salmon is limited relative to that of wild populations, probably as a combined result of founder effects and strong selection in captivity (NOU, 1999). Hence, the genetic future of wild populations receiving intrusions of farmed salmon is likely to be one of lower genetic variability, lower fitness (Hindar *et al.*, 1991; Wang *et al.*, 2002), and higher vulnerability to environmental change (Lande and Shannon, 1996).

The rate of change of genetic variation will be determined in the long term by the level of gene flow from farmed strains to wild populations. To this end, the midpoint of the hybrid group in Figures 1−6 can be used to calculate the average per-generation gene flow (*m*), using recurrence equations for one-way gene flow from Hedrick (1983, pp. 278−280). This midpoint will reflect the proportion of genes coming from either farmed salmon (above) or wild salmon (below), because of the symmetry in how second-generation hybrids and backcrosses to farmed and wild salmon are treated in our model. Using equations for one-way gene flow, the outcome in our "Basic simulation" (no mature parr; Figure 1) corresponds to a per-generation gene flow from farmed to wild salmon of $m = 0.035$, assuming a generation time of four years. Variation in the spawning success of escaped farmed fish (Figure 3) varies this gene flow from 1.5% to 5%. When we include mature male parr in the model, the per-generation gene flow increases to 4.5%, and ranges from 3% to 7% as a result of variation in the survival rates of farmed offspring (Figure 5). These levels of gene flow are similar to those calculated previously (NOU, 1999; Fleming *et al.*, 2000), without information about second-generation effects, and high enough to cause concern for the genetic future of wild populations experiencing average intrusion rates (Tufto and Hindar, 2003).

A question remains regarding strategies to reduce impacts of salmon farming on wild salmon populations: should salmon that are closely related to the native population or that have been fully domesticated be used for farming purposes? The answer is that both carry inherent risks to wild populations. An experiment in the Burrishoole, using a wild population from the neighbouring Owenmore River system, suggested that even this population showed significantly reduced lifetime fitness in the Burrishoole system than the native population (McGinnity *et al.*, 2004). Experiments at Ims with farmed salmon and one of their wild progenitors, the Namsen River (Gjedrem *et al.*, 1991), showed that changes in fitness traits may be caused both by origin and by domestication (Fleming and Einum, 1997; IAF, unpublished). However, it is unlikely that large-scale aquaculture will shift to the use of local, native populations, preferring to continue its programmes of directed selection for commercially valuable traits in farmed salmon, that are not necessarily found in the wild. Thus, a significant reduction in the impacts on wild populations modelled here will be dependent primarily on effective physical or biological containment of farmed fish.

Our model may be a conservative representation of the effects of salmon farming on wild salmon populations. Some genetic and ecological interactions have been investigated in this study, but not disease interactions, which have reduced the numerical size of several populations (Johnsen and Jensen, 1994; Bakke and Harris, 1998; Johnsen *et al.*, 1999; Heuch *et al.*, 2005). Furthermore, we have not modelled the effects of competition from escaped rainbow trout (*O. mykiss*) on wild salmon or the higher propensity of escaped farmed salmon to hybridize with brown trout (Youngson *et al.*, 1993; Hindar and Balstad, 1994). We have modelled direct genetic effects caused by interbreeding, but not the indirect genetic effects caused by reduced population size and new selective regimes (Waples, 1991; E. deEyto, pers. comm.). On the other hand, we have not addressed the possibility that the spawning capabilities of escaped fish may decline in future as a result of further domestication. The combinations of spawning success and survival rates that are most detrimental to wild populations are not always clear, because this depends on the proportion of farmed salmon in the spawning population and on the details of the fitness components (Hutchings, 1991). In our model, variation in survival at the parr stage seemed to have a comparatively large effect, in addition to parr maturity. No other factor, however, seemed to reflect as large variation in impact as that caused by varying intrusion rates (e.g. comparing the Stjørdalselva and Vosso Rivers).

We conclude that the implementation of measures to considerably reduce the number of escaped farmed salmon and their spawning in wild populations is urgently needed. This conclusion is in line with earlier reviews (Hindar *et al.*, 1991; Naylor *et al.*, 2005; Ferguson *et al.*, in press). Our paper provides a quantitative picture of the rapid change likely to occur in many wild populations and of the urgency to find measures to reduce escape rates and to protect wild salmon. It is unfortunate that lessons learned about the effects on wild populations of large stock-enhancement and sea ranching programmes, summarized in two 1980 symposia (Billingsley, 1981; Ryman, 1981), were not considered when developing effective protocols for the salmon farming industry, despite warnings that wild fish would be at risk from large numbers of escaped farmed salmon (e.g. Hindar *et al.*, 1991). Although considerable data have accumulated on interactions between wild and cultured fish during the past 25 years, nothing seems to have invalidated the recommendations made by the 1980 symposia relative to either fish farming or stock enhancement (Myers *et al.*, 2004). Given the length of time and cost of undertaking field experiments limited to a few dedicated facilities, the only realistic way forward is to

continue the development of computer-based predictive models, which allow for risk assessment across the range of escape scenarios. Research into indirect genetic and eco-logical impacts associated with issues such as introduction of disease and effects of density-dependent population dynamics will be necessary components of these future models.

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