

# **Interactive Risk Analysis for Management of Escaped Aquacultured Salmon**

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## **Abstract**

We have developed an interactive model to investigate the risk posed to wild salmon by escaped aquaculture salmon. The model simulates a small population of wild salmon based in a particular stream/estuary/ocean system, into which an aquaculture facility is losing fish to escapes. This system is based on features of the Gulf of Maine salmon streams, and we parameterize the survival characteristics of the wild salmon from the

U.S. Fish and Wildlife Service Report on Atlantic Salmon Stocks in Maine (U.S. Fish and Wildlife, 1999). The survival and reproductive success of escaping smolts is calculated using a within-year physiological model of growth and maturation. Results from the growth model and parameters from the Atlantic salmon report are used in a between-year model predicting the population trajectories of wild and aquaculture fish for two hundred years into the future. The model, written using MATLAB simulation software (Mathworks, Inc., 1984-2002) presents a menu-driven interface that allows the user to investigate different types of ecological interaction scenarios, and different options for management of the escapes. The interactive nature of the model permits a hands-on sensitivity analysis that represents an intuitive way to present information about risks to a non-technical audience. Results from the model suggest the most important parameters to measure in the field.

## **Introduction**

Atlantic salmon are farmed worldwide, both within the North Atlantic, their native range, and in Pacific and Southern Hemisphere waters. They are a tremendous commercial success, and production of aquaculture salmon far outnumbers the natural production of wild salmon (Whoriskey, 2000).

Although derived from wild salmon, aquaculture salmon are not the same as the native species. Wild salmon occur as local populations that generally reproduce in the natal stream in which they originated, and sub-populations of Atlantic salmon differ genetically, reflecting local adaptations for survival (Clegg, *et al*, 2003). The popular

brood stocks of aquaculture salmon are hybrids of European and American origin, and have been selected over generations to enhance their value in the market. While some features, such as fast growth, may enhance their ability to survive in the wild, other features may make them unsuited for the range or environmental conditions that natural salmon populations experience (Fleming, *et al.*, 2002).

When aquaculture fish escape, they represent the introduction of a non-native species, which may have serious ecological effects. These could include competitive or interference effects with wild salmon. If escaped aquaculture salmon become established, they may drive wild populations, already under pressure from habitat destruction and overfishing, further on towards certain extinction. Aquaculture salmon have been found returning to streams in Norway, Iceland, Ireland, and the Canadian east (New Brunswick) and west (British Columbia) (Whoriskey, 2000, Volpe, 2000, and Lacroix and Stokesbury, 2004).

The long-range consequences of ecological interactions between wild Atlantic salmon and escaped aquaculture salmon provides an important framework within which to conduct an ecological risk analysis. Risk analyses are common in engineering and environmental policy (Anand, 2002), often addressing concerns around chemical hazards, but rarely used to evaluate ecological risks to a species or ecosystem. A risk analysis requires specifying the potential states of nature, their probabilities, potential management actions (note that this includes taking no action), and their effects on the states of nature (Anand, 2002). In this case, the states of nature we are interested in are

the kind of interactions that might occur between wild and escaped Atlantic salmon. We have developed an age-structured model of salmon population dynamics to investigate outcomes for a variety of possible interactions. Integral to this model is a physiological model of survival and reproduction potential for escaped aquaculture salmon. That is, we have modeled both within-year individual dynamics and between-year population dynamics.

The model simulates a small population of wild salmon based in a particular stream/estuary/ocean system, into which an aquaculture facility is losing fish to escapes. Given the number of smolts and adults that escape each year, the model calculates the changes in the populations of wild and escaped fish, projecting forward in time from 2000 to year 2100. In addition to investigating a variety of ecological risks, we investigate the impacts of various management decisions in the event of escapes. Management responses to aquaculture escapes include legislative responses, such as mandating containment in the form of secure sea-cages in aquaculture facilities, and responses in the field, such as opening salmon fishing after an escape, to remove the escapees (Goldburg, *et al.*, 2001).

The model was parameterized as much as possible from the Atlantic Salmon Status Review (U.S. Fish and Wildlife Service, 1999). Survival rates, rates of return, and age at smolt transformation are among the values taken from the report.

Information about risks is often supplied to fisheries managers and stakeholders in the form of results from complex mathematical and statistical analyses in which most of the investigation of the problem at hand has been carried out by the authors (Hilborn, *et al.*, 2003). The modeling process (and any implicit decisions about precautionary approaches inherent therein) is far from transparent. However, in contributing scientific advice to discussions of public policy, it is important to avoid an "elitist" stance, and to include stakeholders in the discussion (Anderson, *et al.*, 2003)

Our approach provides an interactive risk analysis tool, to permit those involved in the policy process to conduct their own sensitivity analysis, investigating outcomes over a range of scenarios (Carpenter, 2000). Inquiry-based investigation is a development in science education towards allowing the individual to conduct hands-on experiments with a phenomenon in order to gain a better sense of its character (e.g. Ash and Klein, 1999, Paris, 1997). Central to this concept is the notion of guided inquiry: the person is given a range of ideas within which to form his own questions (Minstrell, 1999). Bringing this approach to a risk-assessment framework can provide better public insight into the science that informs policy decisions. To this end, we imbedded our model in a menu-driven user-interface that makes a wide variety of scenarios and management strategies available for investigation.

We first describe the details of the model and interface, then show results of simulations and sensitivity analyses, and end with a discussion of implications of the model.

## Methods

The following sections describe the three parts of the model: the age-structured population model for wild and escaped aquaculture fish, the within-year physiological model of survival and reproduction for escaped aquaculture smolts, and the user-interface for scenario investigation (Table 1).

**Table 1. Assumptions of the Model**

Characteristic	Description	Nominal Value
Habitat improvement	Freshwater only	1% per year
Fishing	occurs from 1771 - 1985	determines the base population of wild fish
Smolting	occurs after one or two years in freshwater	80% of parr smolt after one year
Adult returns	occur after one (grilse) or two years in the ocean	5% of smolts return after one sea-year.
Survival	Rates depend on life stage	range from 8% - 60%
Escapes	Reproduction of escaped smolts is governed by the physiological model. Escapes begin on Julian day 90 (March 31) and continue throughout the year	20 smolts/year 100 adults/year Catastrophic escapes consist of 5,000 adults and 1,000 smolts.
Freshwater Competition	egg and/or parr	choice of intensities
Competition at sea	We assume (for now) that ocean resources are non-limiting	none
Disease	Seawater (estuarine) out-migrating smolts	10%

*a. Age-structured population model of wild and escaped fish (between-year model).*

The age-structured model is based on annual time steps for wild and escaped fish. The wild fish are assumed to undergo smolt transformation after either 1 or 2 freshwater years and return to freshwater after either 1 or 2 ocean years. As many of the parameters as possible were estimated from data in the USFWS report on the status of Maine salmon (<http://library.fws.gov/salmon>). Values for these parameters and those we estimated are given in Appendix A, Tables 2 and 3. We assume no fishing before 1770, fishing between 1771 and 1985, and no fishing after 1985. We assume that freshwater habitat destruction begins in 1835 and reduces freshwater habitat to 50% of its original value.

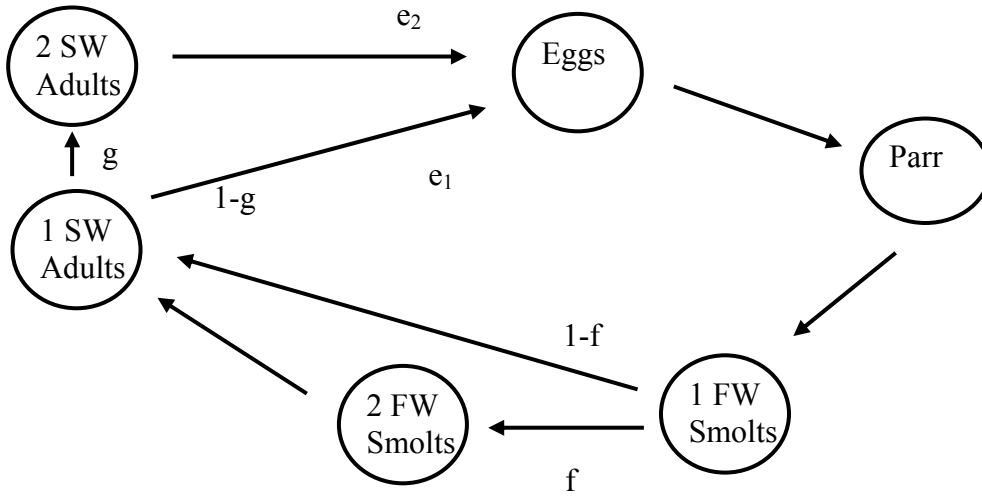
We model risks to the wild population in terms of competitive interactions, disease, genetic introgression, and increased predation on fish due to physical proximity of aquaculture facilities to salmon habitat. These risks may be modified by application of either or both of two management strategies, prevention of escapes or recapture of escaped fish.

**Wild fish**

Competition may occur within the redds (egg competition) and between parr (parr competition). To avoid chaotic dynamics, the competition terms are all of the form  $1/(1+\beta N)$  where  $N$  is the number of individuals at the appropriate life history stage and  $\beta$  is a measure of the intensity of competition. This density dependent term reduces survival from one life history stage to the next. Habitat destruction has a similar effect on reducing survival. We assume that oceanic survival is density independent. Figure 1

illustrates the life cycle of wild fish.

**Figure 1. Life cycle of wild salmon.**



The state variables are

$E(t)$  = eggs at the start of year  $t$

$R_{ij}(t)$  = fish (parr) that will spend  $i$  seasons resident in freshwater who are in the  $j^{\text{th}}$  year of residence at the start of year  $t$ .

$S_i(t)$  = smolts at the start of year  $t$  who spent  $i$  ( $=1, 2$ ) seasons in freshwater.



$A_{ij}(t)$  = fish that spend  $i$  seasons in the sea who are in the  $j^{\text{th}}$  year at sea at the start of year  $t$  (post smolts or adults).

These numerical values represent a relative number of fish, not absolute numbers (i.e., the model doesn't represent a particular stream system with a specific carrying capacity).

Before the introduction of aquacultured fish, the dynamics of the wild stock for eggs is:

$$E(t+1) = e_1 h_f(t) A_{11}(t) \exp(-F(t)) + e_2 h_f(t) A_{22}(t) \exp(-F(t)) \quad (1)$$

where  $e_j$  is the egg production per female for fish who spent  $j$  years at sea,  $h_f(t)$  is the freshwater habitat in year  $t$ , and  $F(t)$  is fishing mortality in year  $t$ .

The parr dynamics are

$$\begin{aligned} R_{11}(t+1) &= \sigma_0 E(t) h_f(t) f \Phi_e(E(t)) \\ R_{21}(t+1) &= \sigma_0 E(t) h_f(t) (1-f) \Phi_e(E(t)) \\ R_{22}(t+1) &= \sigma_2 R_{21}(t) h_f(t) \end{aligned} \quad (2)$$

where new parameters are the maximum per capita survival  $\sigma_0$  and  $\sigma_2$ , the fraction  $f$  of fish that are resident in fresh water for one year and the density dependent competition term for interactions within the redds

$$\Phi_e(E(t)) = \frac{1}{1 + \beta_e E(t)} \quad (3)$$

where  $\beta_e$  represents the intensity of egg competition for resources (e.g., oxygen).

In the case of competition between wild and aquaculture eggs,  $E_a(t)$ , egg competition is

$$\Phi_e(E(t)) = \frac{1}{1 + \beta_e (E(t) + \eta E_a(t))} \quad (4)$$

Here the impact of the aquaculture eggs is modified by  $\eta$ , which ranges between 1 and 1.5 as a user-settable parameter describing the increased effect of competition due to the presence of aquaculture eggs. Setting  $\eta=1$  means that the eggs are equivalent. Larger values for  $\eta$  increase the impact of aquaculture eggs on the survival of all eggs. This term encompasses the idea that aquaculture fish on the spawning grounds may reduce success for all spawners, for example by overlaying redds.

Smolts are produced from the resident fish according to

$$S_1(t+1) = h_f(t) \sigma_1 R_{11}(t) \Phi_r(R) \quad (5)$$

$$S_2(t+1) = h_f(t) \sigma_1 R_{22}(t) \Phi_r(R)$$

where the maximum per capita survival is  $\sigma_1$  and the competition term is

$$\Phi(R) = \frac{1}{1 + \beta_{11}(R_{11}(t) + \gamma R_a(t)) + \beta_{12}R_{12}(t) + \beta_{22}R_{22}(t)} \quad (6)$$

The  $\beta_{ij}$  terms are competition strength for parr of each stage. Aquaculture parr,  $R_a$ , are one-freshwater-year fish, thus competition for them is described by  $\beta_{11}$ . This is modified by  $\gamma$ , analogous to  $\eta$  in the egg-competition term, which ranges between 1 and 3. Here enhanced competition of aquaculture parr reflects their rapid growth relative to wild parr. If there is no competition between wild and aquaculture parr, the equation is modified by the removal of the  $\gamma R_a(t)$  term.

Finally, if  $g_j$  represents the fraction of fish that return after  $j$  years at sea, the adult dynamics are

$$\begin{aligned} A_{11}(t+1) &= r_p \xi_w d_f \sigma_3 h_0(t) [g_1 S_1(t) + g_2 S_2(t)] \\ A_{21}(t+1) &= r_p \xi_w d_f \sigma_3 h_0(t) [(1-g_1)S_1(t) + (1-g_2)S_2(t)] \\ A_{22}(t+1) &= r_p \sigma_3 h_0(t) A_{21}(t) \end{aligned} \quad (7)$$

where  $r_p$  is the fraction of the wild adults escaping impacts of the recapture of escaped fish,  $\xi_w$  is the fraction of smolts surviving enhanced predation,  $d_f$  is the fraction of smolts surviving disease exposure on out-migration (when applicable),  $\sigma_3$  is maximum per capita survival at sea, and  $h_0(t)$  is the habitat at sea at time  $t$ . Disease is assumed to be contracted on out-migration through the estuary, and therefore doesn't affect the  $A_{22}$  fish.

For the case of enhanced predation,  $\xi_w$ , is decreased from 1 to 0.8, which represents the fraction of wild smolts surviving the effects of enhanced predation, assumed to occur as fish are attracted to the vicinity of sea-cages by excess feed in the water. This doesn't affect the  $A_{22}$  adults, who are at sea.

In the case of recapture of aquaculture adults, the wild fish are reduced by a recapture penalty of 5% ( $1-r_p$ ), which represents losses to the wild population due to handling, or mis-identification of wild fish as aquaculture fish.

The fraction of random matings that involve two wild fish is

$$r = \left[ \frac{E(t+1)}{E(t+1) + E_a(t+1)} \right] \quad (8)$$

where  $E(t+1)$  is given by Eqn 1 and  $E_a(t+1)$  is an analogous expression for aquaculture fish. We let  $\rho_a = .3$  denote the probability of assortative mating. The number of eggs produced from assortative wild-wild crosses is thus  $E' = E(t+1) [\rho_a + r(1-\rho_a)]$ , and for the case of genetic introgression, we replace  $E(t+1)$  in Eqn 1 by  $E'$ .

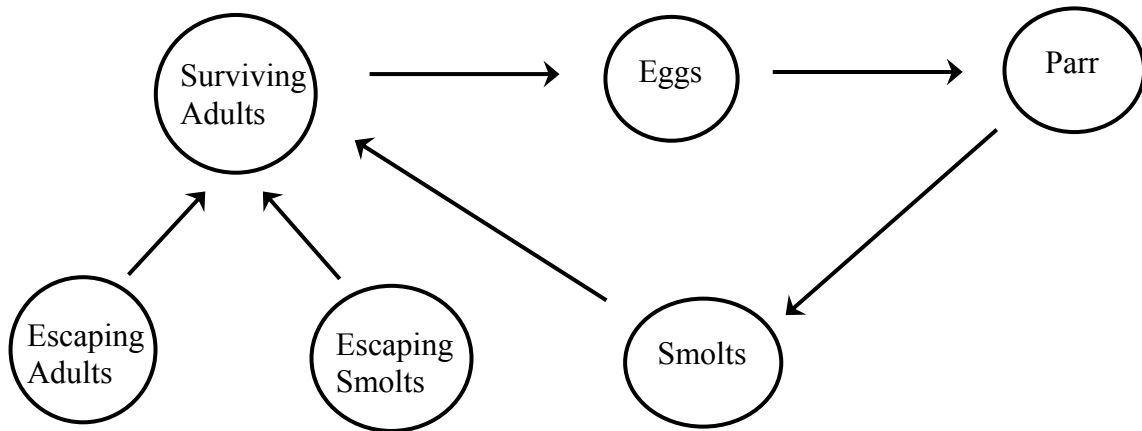
### **Escaped fish**

All escaped fish are assumed to be one year smolts and to be grilse. Each year, 20 smolts and 100 grilse escape from farms, leaking out over the course of the year. This number can be modified by exclusion of either smolt or adult escapes, so that the effect of each

on the wild population can be examined in isolation. Escaping grilse return to the stream the next year and spawn, while smolts may take several years to mature at sea. Survival, reproduction and return of aquaculture smolts are all calculated in the physiological model, described below.

An optional scenario provides for the catastrophic escape of 5,000 grilse and 1,000 smolts in addition to the usual pattern of constant escapes. In this case, we model three pulses of varying duration: a one-year, two-year and five-year pulse, the latter two simulating repeating catastrophes. Figure 2 diagrams the life-cycle of aquaculture fish.

**Figure 2. Life cycle of aquaculture fish.**



Equations for escaped fish are similar to Equations 1-7 for the wild fish, however the escaped fish are assumed to be less-well adapted to local conditions (Fleming, *et al.*, 2000), and are penalized at each stage by a maladaptation parameter,  $\rho_m$ . In the current

model,  $\rho_m$  is same for all stages. Eggs are produced according to

$$E_a(t+1) = \rho_m e_1 A_a(t) \quad (9)$$

where  $\rho_m$  is a parameter describing the maladaptation of aquaculture fish to living in the wild, currently set to 0.3 and applied at each life history stage. In the case of genetic introgression, this is modified so that

$$E_a(t+1) = E_a(t+1) + \zeta(E(t+1) - E') \quad (10)$$

where  $E'$  is as calculated in Eqn. 8, and  $\zeta$  is the rate of survival of hybrid eggs, currently set to 0.5.

Dynamics for aquaculture parr are

$$R_a(t+1) = \rho_m \sigma_0 E_a(t) \Phi_e(E_a(t)) h_f(t) \quad (11)$$

where  $\sigma_0$  is the survival of eggs to parr, and is the same as for wild fish,  $h_f(t)$  is the freshwater habitat in year  $t$ , and the egg-competition term is

$$\Phi_e(E_a(t)) = \frac{1}{1 + \beta_e E_a(t)} \quad (12)$$

except in the case of wild-aquaculture egg competition, in which case Eqn. 4 applies.

The dynamics for aquaculture-derived smolts produced in the stream are

$$S_h(t+1) = \rho_m h_f(t) \sigma_1 R_a(t) \Phi_r(R_a(t)) \quad (13)$$

where  $\sigma_1$  is the maximum per-capita parr-to-smolt survival rate, the same as for the wild fish. If there is competition between wild and aquaculture parr,  $\Phi_r(R_a)$  is given by Eqn. 6; otherwise, it is

$$\Phi_r(R_a) = \frac{1}{1 + \beta_{11} R_a(t)} \quad (14)$$

The escaping aquaculture smolts are given by

$$S_a(t+1) = \Xi S_e \quad (15)$$

which is simply the yearly rate of smolt escape,  $S_e$ , modified by the rate of escape reduction,  $\Xi$ , which may vary between 0 and 100 percent.

The aquaculture adults are calculated as

$$A_a(t+1) = \xi_a(\rho_m \sigma_3 d_f S_h(t) + \Xi A_e) \quad (16)$$

where  $d_f$  is the rate of disease survival of out-migrating hybrid smolts,  $S_h(t)$ , applied in the case of disease transmission,  $\sigma_3$  is survival at sea, and  $\xi_a$  is the rate of survival of aquaculture-derived smolts from enhanced predation.  $A_e$  is the rate of adult escape, which is modified by escape reduction,  $\Xi$ .

Finally, we calculate the contribution of escaped smolts to the surviving population of aquaculture spawners as

$$A_a(t) = A_a(t) + S_a(t-\upsilon) * \Pi \quad (17)$$

where  $\upsilon$  is the reproductive lag (or time-to-maturity) in years for escaped smolts from the physiological model, and  $\Pi$  is their expected reproduction (the product of survival and gonadal weight).

These parameters for escaping smolts are calculated at the beginning of the simulation by the physiological model as a series of probability distributions representing different escape dates throughout the year, and values randomly drawn from these distributions govern expected reproduction each year. This is the only source of stochasticity in the model.



***b. Survival and reproductive potential of escaped fish based on physiological parameters (within-year model).***

We now turn from consideration of populations in competition to the individual growth and maturation of an escaping smolt. We assume that salmonids function according to developmental switches that control gonadal development (Mangel, 1994a, Mangel, 1994b, Thorpe *et al.*, 1998). In the model, the timing of these switches is based on current knowledge of Atlantic salmon in Scotland; we assume that photoperiod is the external cue that synchronizes maturation. We begin with a review of Thorpe, *et al.* (1998), which summarizes the evidence for this.

To reproduce in November, a fish must initiate physiological changes the previous November at which time an individual responds to a developmental switch that determines the maturation process. This is designated by G1. The response involves comparing a combination of the absolute level of lipid reserves and rate of change of lipid reserves with a genetically determined maturation threshold, designated by M1. The justification for such a threshold is that lipids are required for both somatic function during the year and development of gonads (c.f. Henderson and Wong, 1998, Jonsson and Jonsson, 1998) which takes time.

Thus, there is a correlation between the lipid state in the current November and the potential level of reproduction the following November. If the projection based on lipid and rate of change of lipid is less than M1, maturation is inhibited; otherwise gonadal development continues. We assume that the fish assesses current state and rate of change

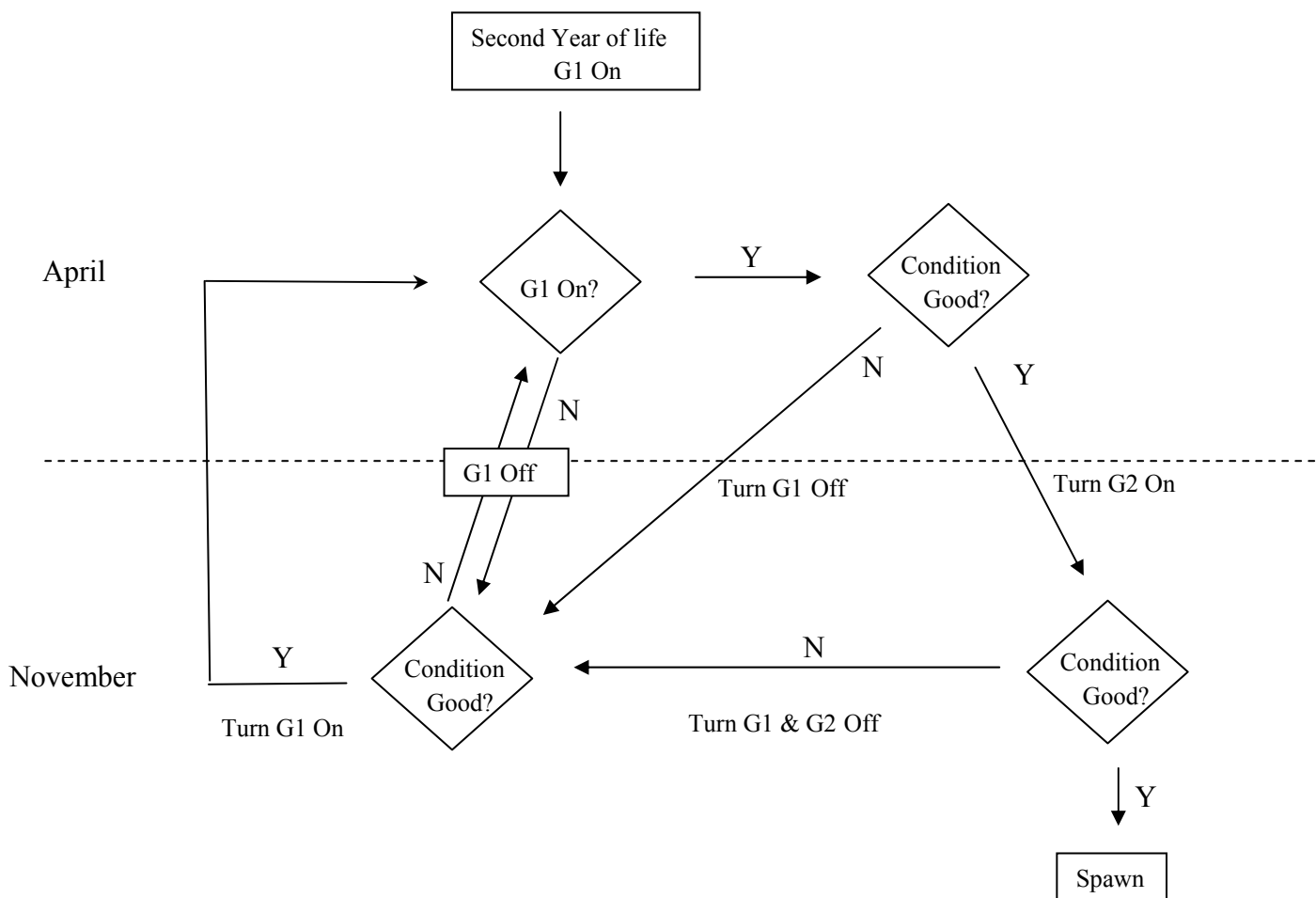
of state and acts on these to the extent that the current values provide information about future ones, using photoperiod as the cue (e.g. Björnsson *et al.*, 1994; Imsland *et al.*, 1997; Forsberg, 1995).

In April, a second maturation switch, G2, occurs and a similar comparison is made between the projection of lipids the following November and a second maturation threshold M2. If  $G1 = 1$  when the combination of lipid and rate of change of lipid exceeds the threshold, then a fish that matures in November has followed the path  $G1 = 1$  the previous November and  $G2 = 1$  the previous April. A fish that does not mature could have followed either  $G1 = 0$  (in which case  $G2$  is also 0), or  $G1 = 1$  but  $G2 = 0$  (in which case  $G1$  is reset to 0). The latter case would arise when growth opportunities exceed the threshold M2 associated with G2.

Since it is possible (through photoperiod and temperature manipulations) to produce fish that mature in the first November of their lives,  $G1 = 1$  at the time of fertilization. Then the first developmental switch the fish will encounter is the G2 switch on Julian day 106 (mid-April). The fish monitors its performance between Julian day 85 and Julian day 106, and based on lipid accumulation rate in that interval and total lipid level, the salmon predicts lipid levels for the following November, Julian day 315. If the predicted lipid levels are below the genetically-determined threshold of M2, the switch remains off ( $G2 = 0$ ), and  $G1$  is reset to zero.

The next switch the fish encounters will be the G1 switch on Julian day 315. Lipid accumulation rate from Julian day 294 – 315, and current lipid levels are used to predict lipid levels for Julian day 471, the following April. If the predicted lipid levels exceed M1, the G1 switch is turned back on ( $G1 = 1$ ), and the fish proceeds to the G2 switch on Julian day 471. Otherwise, the G1 switch is turned off ( $G1 = 0$ ), and the fish must wait an entire year before it can re-initiate maturation. If it decides to mature ( $G2 = 1$  on Julian day 106), it will become anorexic on Julian day 197 of that year and begin to lose weight, but not length. The decision tree for the maturation process is illustrated in Fig 3.

**Fig 3. Decision tree for smolt maturation.**



## Growth Model

The model examines a number of processes in detail, but in the end we are interested only in the survival-to-reproduction of the escaping fish, and the timing of their return to freshwater to spawn. These follow from their physical condition at two points within the year, the spring and fall checkpoints. The following equations govern the genetically-programmed growth pattern of the cultured salmon (weight  $W$ , length  $L$ , and lipid levels  $\Lambda$ ), and determine  $M1$  and  $M2$ .

While immature:

$$W(t) = \left[ W(t-1)^{1/3} + \frac{1}{3} qa(t) \right]^3 \quad (18)$$

$$\log(L(t)) = 1.613 + 0.312 \log(W(t)) \quad (19)$$

$$\Lambda(t) = -0.82 + 0.00418W(t) + 0.000199L(t) \quad (20)$$

Where  $q$  is food finding and processing ability, and  $a(t)$  is food assimilation as a function of temperature, governed by the equation:

$$a(t) = 1 - \left[ \frac{\tau(t) - 6}{12} \right]^2 \quad (21)$$

Temperature,  $\tau$ , oscillates between 8.5° C and 12.5° C, with the peak occurring on Julian day 210.

$$\tau(t) = 10.5 + 2 \cos\left(\frac{2\pi(t - 210)}{365}\right) \quad (22)$$

The clock starts on Julian day 84 in the second year of life, which is the beginning of the window for evaluation of the first G2 switch. Initial weight of the fish is 47 grams, and  $q$  is set to 0.08. From these values, we can calculate the lipid targets for M1 ( $\Lambda(471)$ ) and M2 ( $\Lambda(680)$ ).

Once salmon begin to mature, (Thorpe, *et al.*, 1998)

$$W(t) = \left[ W(t-1)^{1/3} + \frac{1}{3} q c_r a(t) \right]^3 \quad (23)$$

$$\log(L(t)) = 1.556 + 0.323 \log(W(t)) \quad (24)$$

$$\Lambda(t) = -0.82 + 0.00418W(t) + 0.000199L(t) \quad (25)$$

where  $c_r$  is the cost of reproduction, set to 0.988 (Mangel, 1994a). On Julian day 562, under optimal conditions, the salmon will enter the pre-reproduction anorexic period, at which point it will begin losing weight (but not length), and the weight equation changes to:

$$W(t) = W(t-1)(1 - c_a) \quad (26)$$

where  $c_a$ , the cost of anorexia, is 0.001.

The mass of gonads,  $\Gamma$ , at the time of reproduction ( $t = 680$ ) is calculated as:

$$\Gamma(680) = -0.326 + 0.194W(680) \quad (27)$$

The expected reproduction equals gonad mass times expected survival. Expected survival,  $\Omega$ , from the day of escape,  $t_e$ , to day 680 under optimal conditions is

$$\Omega(680) = \exp \left[ - \sum_{s=t_e}^{680} \mu_0 + \mu_1 W(s)^{-0.37} \right] \quad (28)$$

where  $\mu_0$  is the size-independent and  $\mu_1$  the size-dependent component of mortality.

### **Non-optimal case**

To account for the fact that both the environment and the performance of individual fish are variable, we introduce stochasticity into the model by treating weight and  $q$  as variable, and modify the optimal-case equations as follows.

In the weight-gain equations, we separate  $q$  into an individual component,  $q_i$  and an environmental component that can vary over time,  $q_e(t)$ , as per Thorpe, *et al.* (1998).

This results in equations for immature and maturing fish

$$W(t) = \left[ W(t-1)^{1/3} + \frac{1}{3} q_i q_e(t) a(t) \right]^3 \quad (29)$$

$$W(t) = \left[ W(t-1)^{1/3} + \frac{1}{3} q_i q_e(t) c_r a(t) \right]^3 \quad (30)$$

When a fish escapes, the environmental component  $q_e$  changes. In particular,  $q_e = 1$  while in the culture environment, and  $q_e = 0.5$  after the escape. During anorexia,  $q_e$  does not apply, since the fish is not attempting to feed; however we assume those with higher  $q_i$  lose weight at a faster rate, so that the weight equation during anorexia is

$$W(t) = W(t-1) \left[ 1 - c_a \left( \frac{q_i}{q} \right) \right] \quad (31)$$

Finally, we assume that  $q_i$  also affects survival. Higher  $q_i$  will dictate lower survival due to gonadal steroids interacting with the immune system (Mangel, 1994), and behaviours such as increased risk-taking to acquire food. The new survival equation is

$$\Omega(680) = \exp \left[ - \sum_{s=t_e}^{680} \left( \mu_0 + \mu_1 W(s)^{-0.37} \right) \left( 1 + c_g \left( \frac{q_i - q}{q} \right) \right) \left( 1 + c_w \left( \frac{q_i - q_w}{q_w} \right) \right) \right] \quad (32)$$

The growth penalty  $c_g$  applies throughout the life of the fish, while the wild penalty  $c_w$  applies after the escape. Optimal  $q$  for life in the wild,  $q_w$ , is different than the optimal value in the aquaculture environment. We set  $c_g = 0.8$ ,  $c_w = 0.8$ , and  $q_w = 0.9q$ .

### Decision points

With a given initial weight and a given  $q_i$ , we can predict an individual's maturation date and expected reproductive success. In the 21-day evaluation period before a trigger date  $T$  (day 106 for G2 and day 315 for G1), we measure performance as

$$\kappa_i = \left( \frac{1}{21} \right) \sum_{s=(T-21)}^T \frac{\psi_i(s)}{\psi(s)} \quad (33)$$

where  $\psi_i(s)$  and  $\psi(s)$  are the actual and genetically-expected daily specific growth rates, calculated as

$$\psi(s) = W(s-1)^{-2/3} (W(s) - W(s-1)) \quad (34)$$

$W(s)$  is either the genetically-expected or the actual weight, depending on whether  $\psi(s)$  or  $\psi_i(s)$  is being calculated. On the trigger day  $T$ , at the end of the assessment window, weight, length and lipids are predicted for the next trigger date (either 209 days later for G2 or 156 days later for G1). Predicted weight  $W_p$  is a function of performance for both immature (Eqn 18) and maturing fish.

$$W_p(t) = \left[ W_p(t-1)^{1/3} + \kappa_i \frac{1}{3} q \Phi(t) \right]^3 \quad (35)$$

$$W_p(t) = \left[ W_p(t-1)^{1/3} + \frac{1}{3} q c_r \Phi(t) \right]^3 \quad (36)$$

The predicted weight for the first day of the projection period is the actual weight of the fish on that day. For prediction, we use the genetically-encoded  $q$  rather than the individual-specific  $q_i$ .



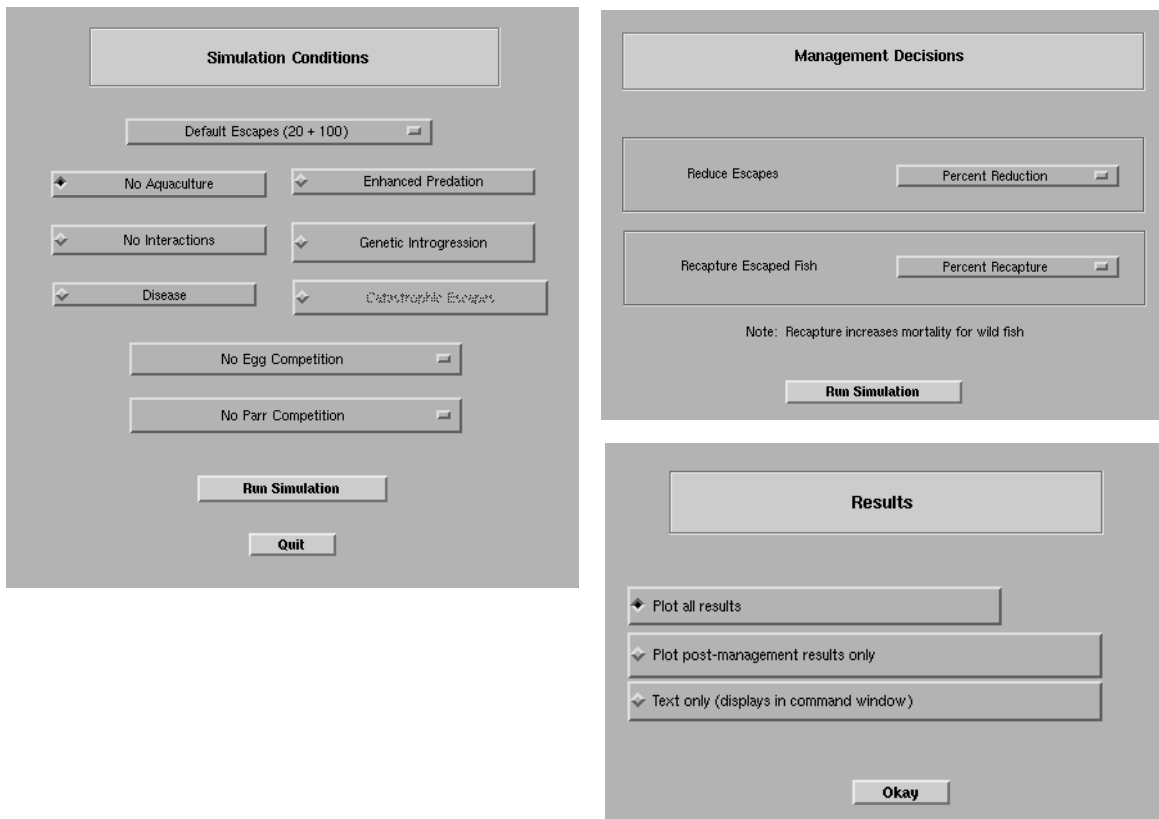
From the predicted weight, we calculate predicted lengths and lipids for the trigger dates according to the appropriate equations for the immature/maturing fish. If predicted lipids are greater than the target value M2 for the G2 trigger date, then the *in silico* fish matures, otherwise both G2 and G1 are zero. If predicted lipids are greater than the target value M1 for the G1 trigger date, then  $G1 = 1$ , and the fish proceeds until it approaches the G2 trigger day again.

For a given initial weight,  $q_i$ , and day of escape, we calculate the day on which the individual will reproduce, as well as its expected reproductive success and whether it survives to reproduction. We assume that initial weights are drawn from a normal distribution,  $N(47, 2.66)$ , and  $q_i$  is drawn from  $N(0.08, 0.09)$  that is truncated at zero and re-normalized. Survival and reproduction calculated from these equations are used to parameterize the age-structured model for escaped smolts, and the day of reproduction is used to determine the size of the lag between escape and reproduction. Parameters for the physiological model are in Appendix A, Tables 4 and 5.

### *c. Menu-driven interface*

The model is driven by a series of menus used to define simulation conditions, management conditions, and the display of results (Figure 4). New scenarios may be explored repeatedly.

**Figure 4.** The graphical user interface.



### **Interactions**

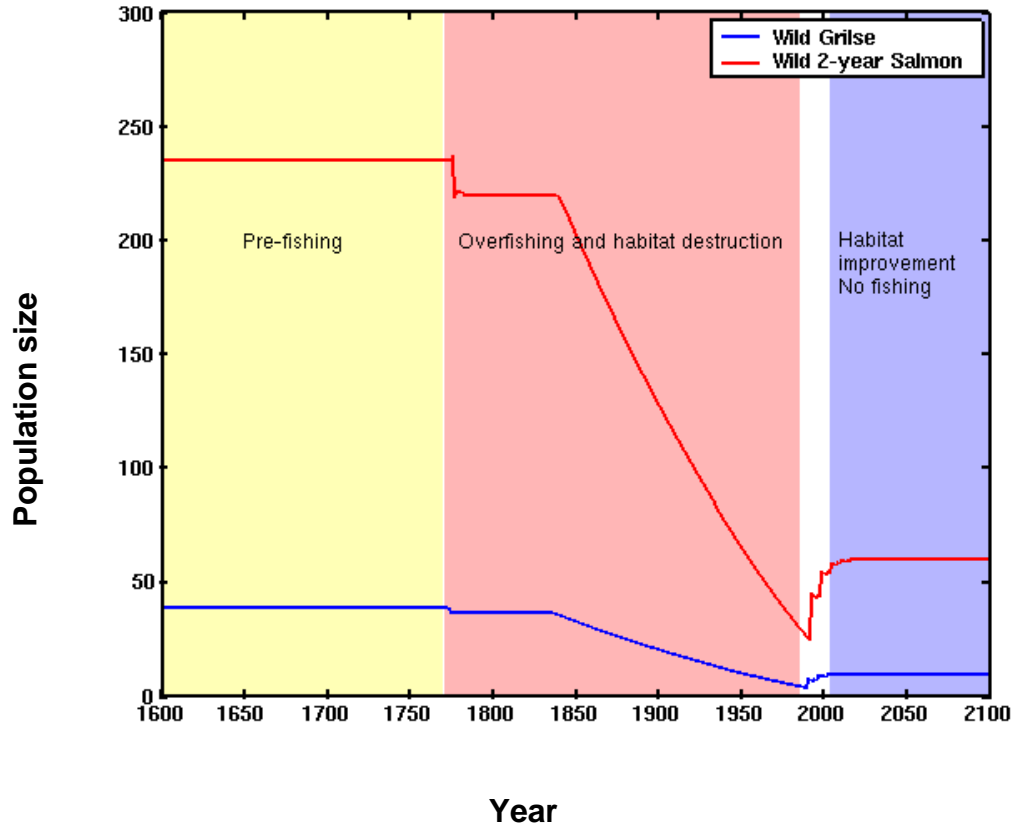
The ecological scenarios available fall into two categories. Scenarios in which no interactions occur between the wild and farmed fish can be explored with or without aquaculture escapes occurring. Interaction scenarios, such as Egg or Parr Competition or Genetic Introgression, can occur in any combination, or all together.

**No Aquaculture:** The output of the model is the trajectory of wild stock in the absence of aquaculture. In this case, no management actions are considered, and the output of the model is a plot of the populations of adult salmon and grilse from the year 1600 to the year 2100. The plot shows the draw-down of the population from fishing and habitat loss, followed by recovery projected to occur between 2000 and 2100 (Figure 5).

**No Interactions:** The output of the model is the trajectory of wild stock and aquaculture stock given that escapes are occurring, but no specific interactions apply. However, escaped fish survive and reproduce, and their existence dilutes the fraction of the population that are wild salmon.

**Egg Competition:** The output of the model is the trajectory of wild stock and aquaculture stock given that egg competition is occurring in the redds, leading to fewer hatchings of wild fish. This parameter can be set to any of {none, low, medium and high} values.

**Figure 5.** Model results for wild salmon in the absence of aquaculture.



**Parr Competition:** The output of the model is the trajectory of wild stock and aquaculture stock given that parr compete for resources in the streams, affecting parr survival. This parameter can be set to any of {none, low, medium and high} values.

**Enhanced Predation:** The output of the model is the trajectory of wild stock and aquaculture stock given that there is predator attraction to the mouths of rivers due to aquaculture and thus enhanced predation on both wild and escaped smolts.

**Genetic Introgression:** The output of the model is the trajectory of wild stock and

aquaculture stock given that there is genetic introgression caused by mating between wild and aquaculture fish. The offspring of crosses between wild and aquaculture fish are tracked as aquaculture fish. Only the offspring of two wild parents are considered wild fish.

**Disease:** The output of the model is the trajectory of wild stock and aquaculture stock given that out-migrating smolts are attracted to aquaculture facilities because of abundant food concentrations in the water, and they contract a disease from proximity to the penned fish, which kills them. Currently, 10% of smolts are affected by disease.

**Catastrophic Escapes:** This option is only available if an interaction scenario has been chosen. Aquaculture escapes occur as usual (100 adults and 20 smolts) in most years. In year 2030, instead of the regular numbers, 5,000 adults and 1,000 smolts escape. This large escape is repeated in 2060 and 2061, and then again in each year between 2080 and 2085.

### **Management Options**

**Adult recapture:** The model predicts the trajectory of wild stock and aquaculture stock under the ecological scenario defined by selected interactions. The rate of recapture may be chosen to be between 10% and 100%. Recapture causes an additional mortality on wild stocks proportional to the rate of recapture, up to 5% for 100% recapture. Note that because recapture is of returning adults, but both smolts and adults escape, that even with 100% recapture there will still be aquaculture fish at the end of the simulation,

representing those smolts that have escaped and not yet returned to be captured.

**Reduced escapes:** The model predicts the trajectory of wild stock and aquaculture stock under the ecological scenario defined by selected interactions. The amount of escape reduction may be selected to be between 10% and 100%.

### **Results options**

The third menu is for selection of output options, shown in Figure 5. The three options are:

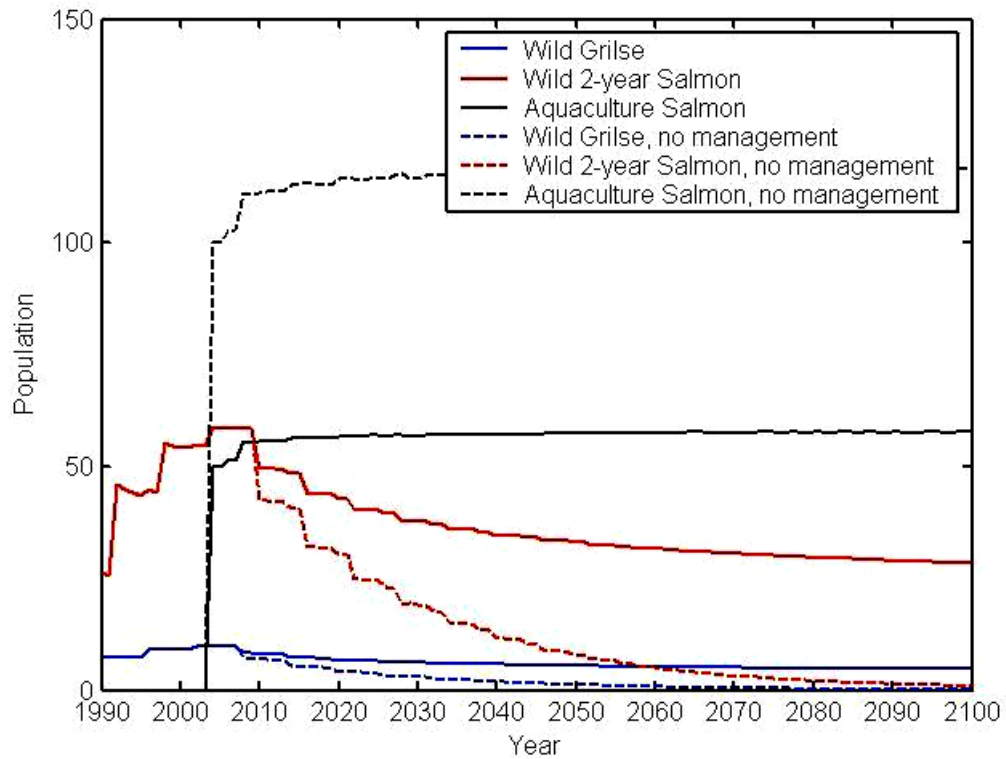
- Text Only  
A text description of the scenario and outcome are displayed in the Matlab command window
- Plot post-management results  
A text description of the scenario and outcome are displayed in a results window, and trajectories are plotted for the populations under managed conditions
- Plot All results  
A text description of the scenario and outcome are displayed, and trajectories are plotted for the pre- and post-management results

The results options are only offered when the first simulation is run.

Once a scenario, management and results options have been chosen, the simulation is run

and results are displayed as a paired set of panels, one with a text description of the scenario and results, and the other a plot of the population trajectories. Figure 6 shows the resultant display from a managed scenario, with all results plotted.

**Figure 6. Example results from a managed scenario.**



Simulation conditions:

Parr competition low  
Genetic introgression

Management actions:

Escape reduction                      50 %

Fish stocks in year 2100 (no management):

Wild	Farmed
1.04324	116.73

Fish stocks in year 2100 (with management):

Wild	Farmed
33.052	57.9497



## Results and Discussion

The model results show that the final population of aquaculture salmon in the stream is closely tied to the number escaping. Table 2 shows the 2100 populations of the wild and aquaculture adult spawners under each individual scenario, given no management, with 50% escape reduction, and with 50% recapture. Numbers of aquaculture salmon at the end of the simulation are close in each case to the number of unrecaptured escapees except under the “Enhanced Predation” scenario.

**Table 2. Populations of adult spawners returning to freshwater in year 2100.**

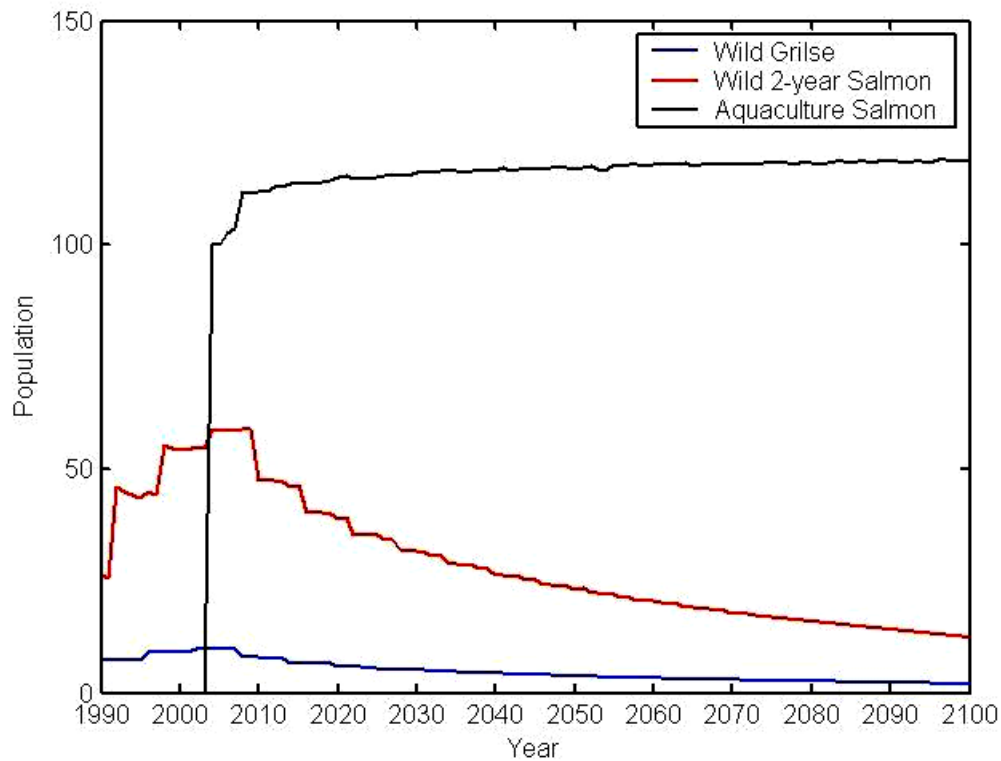
	<u>No Management</u>		<u>50% Recapture</u>		<u>50% Reduction</u>	
	Wild	Farmed	Wild	Farmed	Wild	Farmed
<b>Genetic Introgression</b>	14.41	118.52	45.61	55.97	49.24	57.22
<b>Egg Competition (low)</b>	43.33	108.22	54.27	54.82	56.93	54.06
<b>Enhanced Predation</b>	50.18	65.87	48.15	34.34	50.18	32.59
<b>Disease</b>	60.35	97.65	58.06	49.58	60.35	48.57
<b>Parr Competition (low)</b>	63.97	108.12	64.66	54.78	67.25	53.93
<b>No interactions</b>	70.52	110.54	67.98	55.9	70.52	56.46

Table 2 also shows that the management strategy of reducing escapes is marginally better than that of recapturing escapees for increasing the survival of the wild fish.

For the parameters used here, scenarios affecting successful egg production are the most critical for the survival of the wild salmon. Genetic introgression has the greatest effect

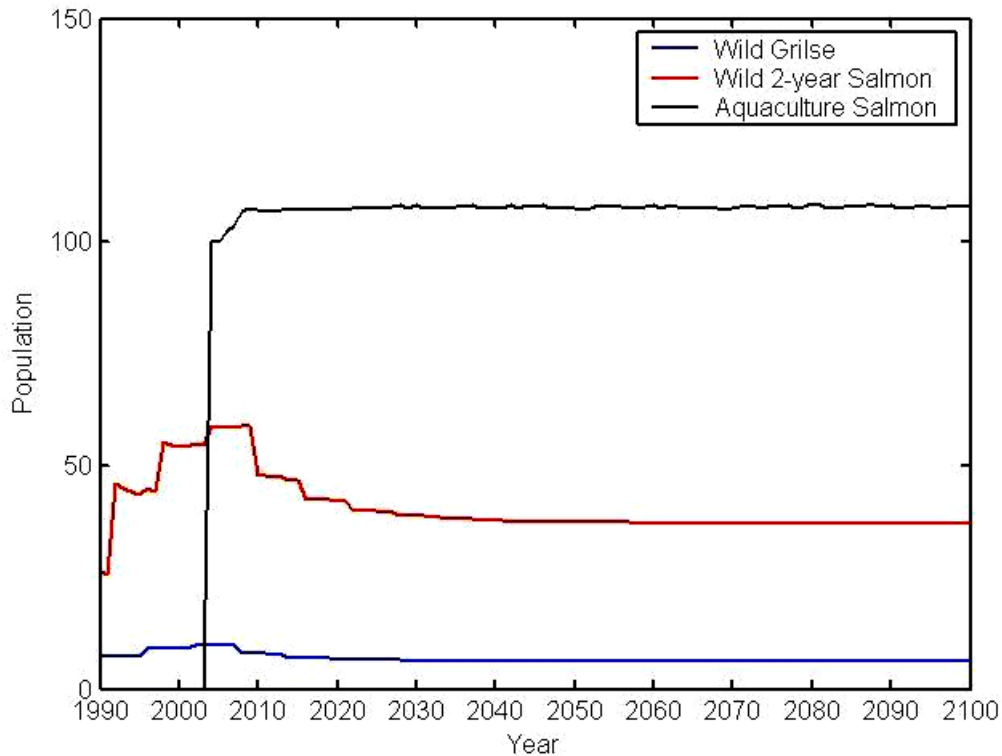
on the wild population, and is the only scenario in which the trajectory of the populations doesn't equilibrate within the simulation period (Figure 7). Wild populations continue to decline, while the aquaculture fish show a slight increasing trend.

**Figure 7. Population trajectories under the “Genetic Introgression” scenario.**



Egg competition, the result of non-hybridizing adult interference in the spawning process – such as redd destruction – is also quite harmful to the wild population. Figure 8 shows population trajectories under “low” levels of egg competition.

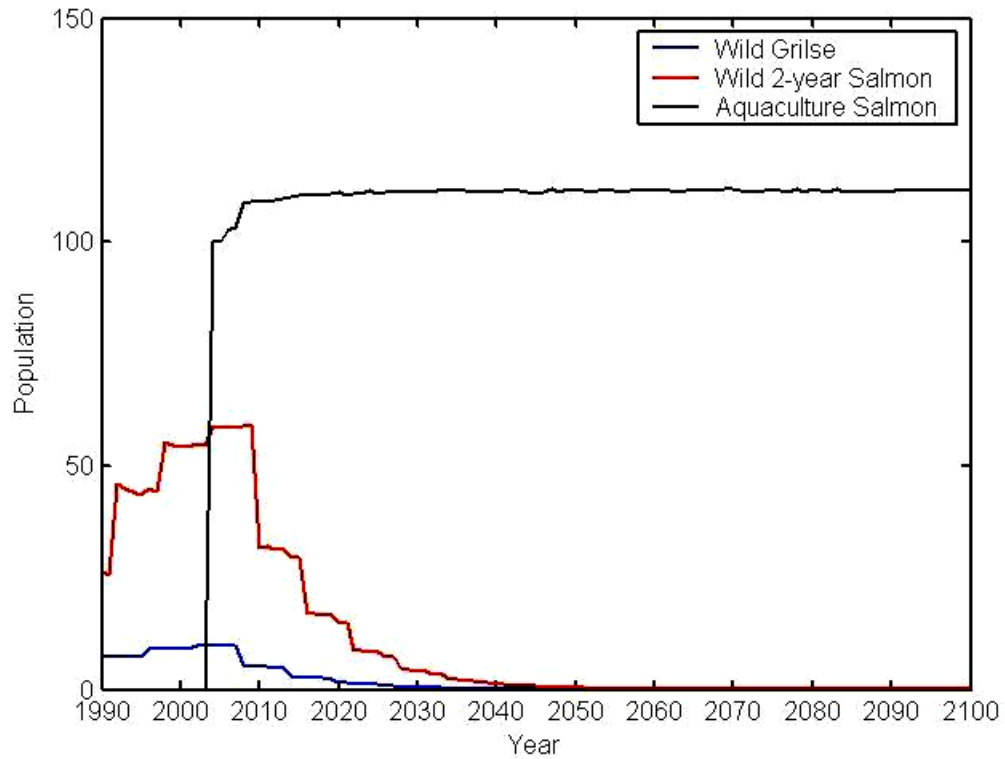
**Figure 8. Population trajectories for low levels of egg competition.**



The pattern of population change in Figure 8 is characteristic of the scenarios not involving genetic introgression: all equilibrate around year 2040, although at different values (Table 1).

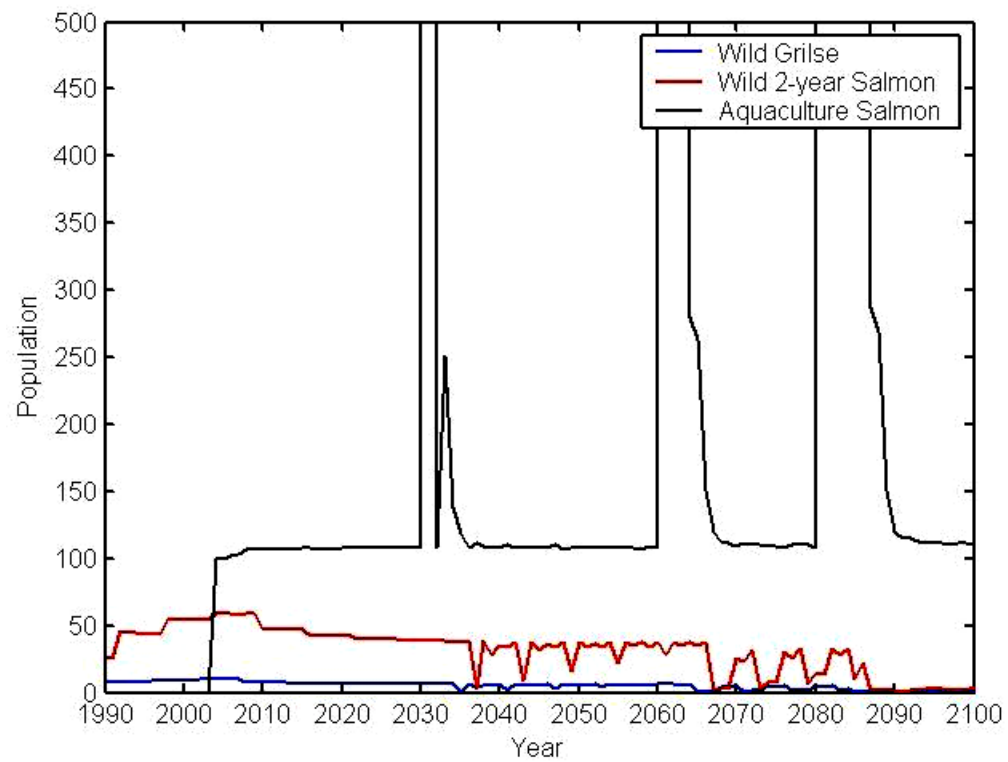
Combining scenarios can drive the wild fish to extinction. Figure 9 shows the result of combining genetic introgression with medium levels of egg competition. Extinction here occurs around year 2045. With lowered competition, it occurs at year 2050 and at the highest level of egg competition, the wild population is extinct by 2040.

**Figure 9. Combined introgression and egg competition (low).**



Finally, the advantage of a staged life history is shown in the resilience of the wild population in the face of catastrophic escapes (Figure 10). The fact that only the freshwater stages are impacted means that the adult salmon at sea are able to replenish the stream population after a crisis.

**Figure 10. Low egg competition with catastrophic escapes of 5,000 adults and 1,000 smolts in years 2030, 2060 and 2061, and 2080-2085.**



## Conclusions

This model uniquely brings together three very different concepts: the life-history variation of the physiological model, age-structured vulnerability, and an interface for investigation of different ecological scenarios. The stochastic physiological model expresses our uncertainty about the success of the aquaculture fish. The age-structured model allows us to investigate the differences in vulnerability of wild fish at different ages, and in different environments.

Genetic introgression, egg- and parr-competition all represent threats occurring in freshwater, as does habitat loss, which limits the maximum size of wild populations (Fig. 5). Enhanced predation, disease, and recapture strategies affect post-smolts and adults, ocean-resident fish. Wild salmon are much more vulnerable to freshwater threats than to the ocean effects modeled here. This would suggest that effective management should focus on keeping aquaculture fish out of the freshwater environment, once they have escaped.

Since realistic fishery models depend on numerous arbitrary choices (Schnute, 2003), models such as this one should serve as tools for thought, and contribute to a frank discussion of the options (Schnute and Richards, 2001). There is an increasing trend towards developing cooperative practices in management by working with stakeholders – the North Atlantic Salmon Conservation Organization (NASCO) is an example of one such (international) effort. It is also increasingly important that we provide full disclosure about scientific uncertainty and unknowns (Stephenson and Lane, 1995),

which as one of us has noted elsewhere, is rarely fully understood or appropriately used in policy discussions (Rosenberg, 2003). The interface we present here is an attempt to permit non-technical parties a window into analysis of unknowns.

Lackey (2003) and others argue that policymakers and stakeholders need to be informed about the assumptions of the model. Our interface allows the user to make his own assumptions about likely scenarios, and then investigate outcomes over a range of inputs. Precautionary approaches to management require an assessment of risk, and this model is an effort to make risk assessment an open process through much-needed user-friendly software (Harwood and Stokes, 2003). We hope to see this approach widely adopted.

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## Appendix A. Model Parameters

The parameters we used for the between-year model of salmon populations are shown in Tables 2 and 3. Those in Table 2 are from the U.S. Fish and Wildlife Atlantic Salmon Stocks report (U.S. Fish and Wildlife, 1999). Values in Table 3 were estimated. Critical points in the timeline for the physiological model are shown in Table 4. Parameters used in the physiological growth model are given in Table 5.

**Table 2. Parameters from Atlantic Salmon report.**

Survival parameters	
$\sigma_0 = .08$	Average survival to fry * Average survival to parr
$\sigma_1 = .5$	Survival to 1 <sup>st</sup> -year smolt
$\sigma_2 = .6$	Survival a second year in-stream
$\sigma_3 = \sqrt[3]{.1}$	Ocean year survival rate
Life history parameters	
$f = .8$	Percent of parr that smolt after 2 years
$g_1 = 0.05$	One-year smolts that return as grilse
$g_2 = 0.05$	Two-year smolts that return as grilse
$e_1 = 5400$	Egg production of a 1-SW female
$e_2 = 7200$	production of a 2-SW female

**Table 3. Estimated parameters (default values for “low” competition).**

Competition coefficients	NB: Coefficients apply to wild and aquaculture fish
$\beta_e = 0.000005$	Egg competition
$\beta_{11} = 0.0001$	One-freshwater year smolts
$\beta_{21} = 0.0001$	Two-freshwater year smolts in their first year
$\beta_{22} = 0.0001$	Two-freshwater year smolts in their second year
Aquaculture parameters	
$\zeta = .5$	Cross-survival of hybrid eggs
$\rho_m = .3$	Penalty for maladaptation
$\rho_a = .3$	Probability of assortative mating
Scenario-dependent	
$r_p = 0.05$	Mortality of wild fish due to recapture
$\xi_w = 0.8$	Survival of wild fish from enhanced predation
$\xi_a = 0.6$	Survival of aquaculture fish from enhanced predation
$d_f = 0.1$	Loss of smolts to disease
Initial wild populations	
$A_{11} = 30$	Grilse returning to spawn
$A_{22} = 220$	Two-seawinter adults returning to spawn

**Table 4. Timeline for maturing smolts**

Julian day	
84	Day 84 in second year of life; first day of the simulation
106	Evaluation point for maturation the following November
197	Onset of anorexia for a fish maturing in November
315	Evaluation point for maturation in November of the third year
680	Day of reproduction

**Table 5. Parameters for the physiological model**

Parameter	
$q = 0.08$	Ability to find and process food
$q_e = 1 \text{ or } 0.5$	Environmental component of $q$ ; changes with escape
$q_i =$	Individual component of $q$ ; drawn from a Normal(0.08,0.09)
$q_w = 0.9q$	Optimal value of $q$ in the wild
$c_a = 0.001$	Cost of anorexia
$c_r = 0.988$	Cost of reproduction
$c_w = 0.8$	Penalty for living in the wild after escape
Initial weight	Drawn from a Normal(47, 2.66)