

Modelling of impacts

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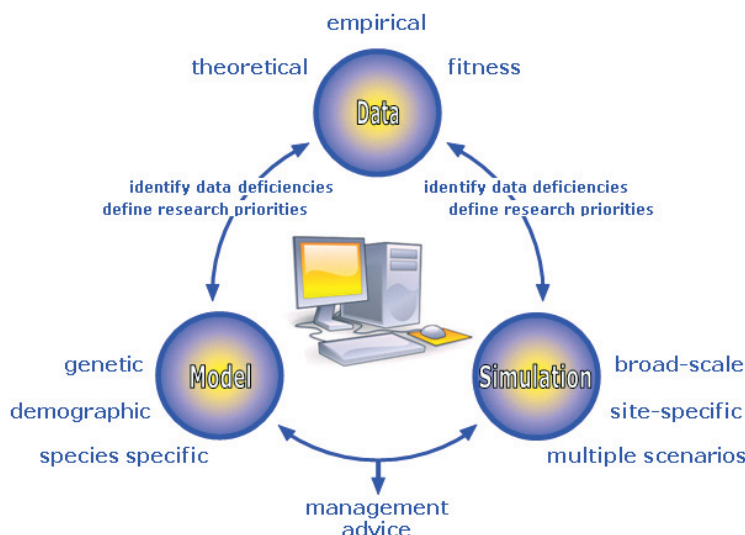
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The modelling approach

Empirical studies comparing the fitness of wild and escaped farmed stock, whilst essential for providing baseline measurements of individual and population level fitness, are very expensive and time consuming to perform, particularly for the many species that are undergoing increases in production. It is also difficult to extrapolate from these studies to different mixing and population specific scenarios. Computer-based models of population mixing help overcome these problems. They can be used to simulate ecological and genetical interactions between farm and wild fish for a range of conditions, and provide insight into the potential consequences for population character and abundance. This can be achieved by models which include both demographic and genetic parameters. The basic modelling approach is outlined in Fig 1.

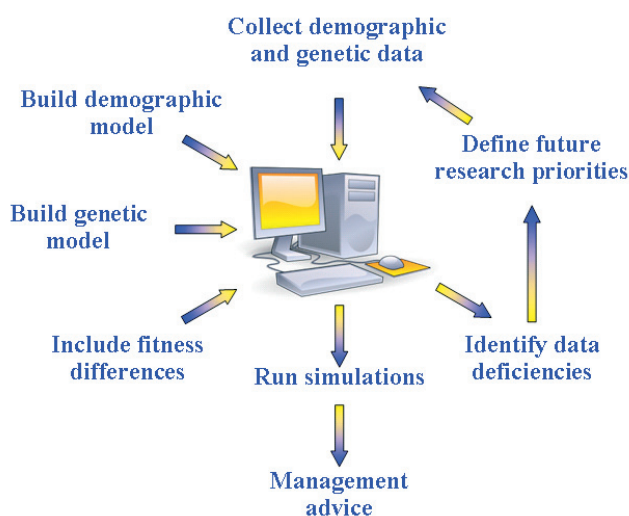


Fig. 1. Basic steps in the development of a culture/wild interaction model.

Existing modelling work

Finfish

To date, interaction models have been restricted to salmonids. Hutchings (1) modelled the threat to wild populations experiencing various intrusion rates of escaped farmed salmon and small or large fitness differences among the offspring. In Hindar *et al.* (2), fitness is presented by life-history stage in a fitness component analysis, and the range of scenarios narrowed down based on the whole-river experiments in Ireland and Norway (3, 4, 5). The model of Hindar *et al.*, focused on the effects of interbreeding and varying fitness parameters between different offspring groups (Wild x Wild, Hybrid, Farm x Farm), and how these parameters may affect the group proportions through time. The model consists of three main elements:

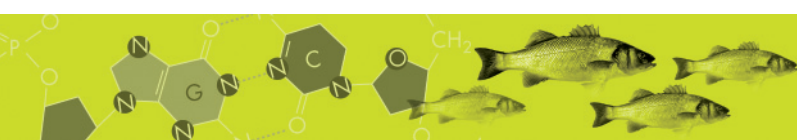
1. Intrusion. The annual intrusion rate of escaped farmed salmon into the spawning population. This rate can be assumed to be fixed, or it may vary from season to season according to time series observations or some stochastic process. Whether the farmed salmon escaped early or late are considered.
2. Spawning. The relative spawning successes of the different groups, including mature male parr, can be varied. Sex ratios, size differences etc. can also be considered in the model.
3. Survival. The offspring groups have varying relative survival rates for different life-history stages.

The basic simulation, with a fixed intrusion rate of 20 % escaped farmed salmon in the spawning population and average fitness parameters, suggests that substantial changes take place in wild salmon populations within ten salmon generation (~40 years). Low-invasion scenarios suggest that farmed offspring are unlikely to establish in the population, whereas high-invasion scenarios suggest that populations are eventually composed of hybrid and farmed descendants. It was concluded that further measures to reduce escapes of farmed salmon and their spawning in wild populations are urgently needed.

Transgenic fish

Transgenic fish strains have been in development since the mid 1980s, but as yet, none are known to have entered natural ecosystems. Nevertheless, a major objective of some transgenic fish research is development for aquaculture of strains with enhanced production characteristics such as improved growth rates and feed-conversion efficiencies (6). Significant concern has emerged regarding potential ecological effects of transgenic fish in the wild as well as approaches and uncertainties associated with risk assessment methodology (6, 7, 8). Developing accurate modelling approaches to estimate the consequences of transgenic fish in nature is therefore essential to assist with their safe application in the future and this is perhaps the best modelled area of possible cultured/wild genetic interactions.

Several deterministic models have been developed to explore variables which may influence the persistence of a transgene in fish populations (9, 10). These modelling exercises revealed that from a practical perspective, releasing transgenic individuals with multiple transgenic loci could significantly reduce the number of generations required to establish the transgene in 99% of individuals in a population, and that such effects are more pronounced when stocking densities are less than 40% of the natural population size. It was also found that the speed of transgene introgression could be underestimated if factors such as variable clutch size and survival to maturation were not considered, particularly in species with short life cycles.



Models have also examined the influence of fitness effects of transgenic fish (11). It was found that higher rates of introduction elevated transgene equilibrium frequency in populations when the transgene confers a deleterious effect. In cases where a hemizygote advantage exists, wild type fish persist in the population and the transgene reaches a maximum equilibrium frequency of 0.5 (lower in cases where fitness differences exist between homozygous transgenic and wild-type fish).

Models incorporating effects of multiple fitness parameters and life history characteristics on both transgene frequency and population size have also been developed (8, 12). A range of outcomes have been predicted using these models, depending on the interaction scenarios examined. Reductions in transgene viability or enhancement of male mating success could respectively eliminate or drive to fixation a transgene in populations, with minimal effects on population size. In contrast, combining negative and positive fitness values could have very profound effects on fixation and population size, perhaps even ultimately driving the population to extinction. This consequence has been termed the Trojan gene effect (for example see Fig.2).

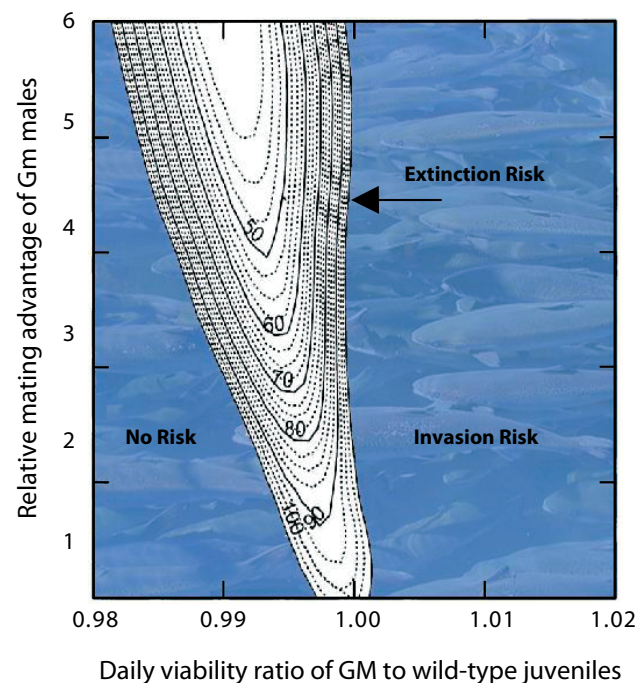


Fig. 2. Predicted time to extinction in generations (contour lines) as a function of the ratio of GM to WT daily juvenile viability and GM male mating advantage relative to WT males (after 13).

Shellfish

To our knowledge, there is currently no modelling study dealing with the risk of genetic impacts of cultured shellfish stocks on wild populations. Most existing modelling studies on cultured shellfish species focus on bivalve molluscs. They primarily deal with population interactions with the environment, and are used to assess the carrying capacity of a studied ecosystem (typically a bay, estuary or lagoon) in terms of aquaculture production, and to optimise rearing practices and management techniques (14, 15, 16). Most of these models are based on a rather precise description of the environment through the simulation of the spatio-

temporal dynamics of hydro-biological conditions. The environmental module is then coupled with a module simulating bivalve physiology and bioenergetics that determine individuals' life history traits and in turn their population dynamics (15, 17). Most of these modelling studies deal with monoculture but a few models account for polyculture (15, 17). The latter would be a good starting point for modelling the interaction between cultured stocks and wild populations since in mathematical terms modelling several populations is rather similar to modelling several species.

Development of new models: a framework following the development of an individual-based model of Atlantic salmon interactions

The development of interaction models for many of the species in aquaculture benefits greatly from the experience of pre-existing models. One such model is the recently developed individual-based model of cultured/wild interactions in the Atlantic salmon (18, 19). The steps used in the production of this model follow those outlined in Fig. 1 and provide a framework for building interaction models with other species. The novel genetic component of this model, linking genotype to phenotype over many generations, could also be of particular benefit in the examination of other species.

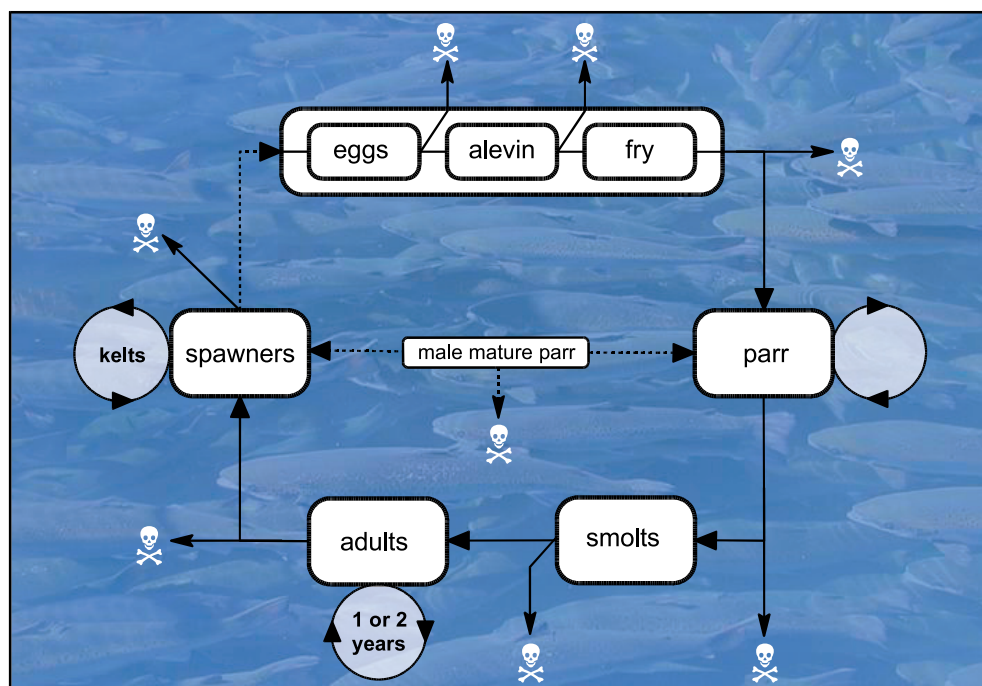
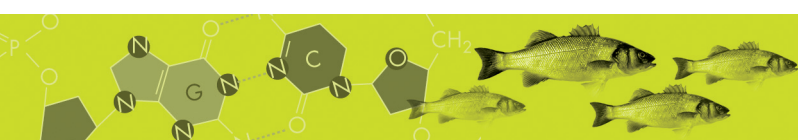


Fig. 3. Demographic life-cycle model of an Atlantic salmon population.

Demographic model

Data is collected from the literature detailing the life-history and demographic interactions of a wild individual/population. A life-cycle model is then built in the computer (Fig. 3), and parameterized using the information collected. The model follows individuals from egg, through the various developmental stages, until post-spawning death. As an individual moves between stages, growth and the probabilities of maturation and survival are calculated for each fish. These are based on a synthesis of population demographic parameters collected from the literature and weighted by the various individual trait values of a particular fish. The model is then



corroborated against empirical observations under a number of different scenarios to make sure it is capable of realistic representation of an unimpacted wild population. This stage gives an ideal opportunity to systematically examine the availability of data describing the various parameters involved, and thus to identify any gaps and define research priorities. During the development of the salmon model (18) the need for further information on the various density dependent processes acting in the freshwater juvenile phase was identified, and research projects were begun to examine these factors.

Fitness differences

In order to model the influence of escaped cultured stocks on the wild population, the demographical, behavioral and fitness differences between wild and escaped cultured individuals must be collected/determined. Again, this procedure allows the identification of knowledge gaps, and the defining of research priorities. Monitoring in wild scenarios is one tool to examine these influences, but of particular use here is the use of ‘common-garden’ experiments. These are experiments where mixing scenarios are initiated in the wild, and the population/s monitored over multiple generations, with the measurement of many individual and population parameters. During the development of the salmon model invaluable data was collected from the common-garden experiments carried out in both Ireland (3, 4) and Norway (5) (see Fig.4), and similar data must be collected for parameterisation of models for other species.

Trait	Gene complex/ fitness influence	Scaled to wild			Fitness Differential
		Wild	F ₁	Farmed	
Egg survival to hatch (%)	embryonic	1		0.333	-66.67
Alevin size at first feed (mg)	embryonic	1		0.888	-11.22
0+ size (mm)	embryonic	1	1.146	1.171	+17.05
1+ size (mm)	freshwater	1	1.174	1.145	+14.52
Egg to smolt survival (%)	freshwater	1	0.615	0.410	-59.00
Smolt age	freshwater	1	0.798	0.637	-36.31
Mature male parr at 0+ (%)	freshwater	1	0.722	0.778	-22.22
Mature male parr at 1+ (%)	freshwater	1	0.667	0.232	-76.81
Relative male parr reproductive success	freshwater	1	2.237	3.953	+295.26
Smolt to adult survival (%)	marine/adult	1	0.850	0.333	-66.67
1SW length (mm)	marine/adult	1		1.127	+12.70
Sea age (% 1SW)	marine/adult	1		0.141	-85.86
Relative mature male reproductive success	marine/adult	1		0.2	-80.00
Fecundity (egg no) ⁴	marine/adult	1		1.290	+29.04
Egg size (mm)	marine/adult	1		0.972	-2.76

Fig. 4. *Fitness differentials associated with various life-history stages of Atlantic salmon based on published empirical measurements. Population measurements are compared to a wild type scaled to 1. Fitness Differential is the percentage difference in farmed compared to wild fish (for references see 19).*



Genetic model

The underlying genetic architecture and gene/allele interactions of quantitative fitness traits are often extremely complex, and include additive, dominant, and epistatic influences (20). Although there is little information as to the relative importance of each of these influences, empirical observations suggest that a large proportion of the genetic basis for fitness in salmon can be described by a simple additive model (4) and this additive genetic model was therefore used in the novel genetic component of the salmon interaction model (19).

The second component of the genetic architecture that must be modelled is the distribution of genetic effects across the number of loci influencing the quantitative trait. These effects were modelled using an exponentially declining effects distribution model (21). Hayes and Goddard (22) carried out a meta-analysis of QTL mapping studies in livestock to infer the distribution of the effects of genes. They found the distribution of QTL effects was moderately leptokurtic, with many QTL of small effects and a few of large effect, consistent with the exponentially declining theoretical model of QTL influences. Similar evidence for the exponentially declining effects model has also been seen in salmonids (23).

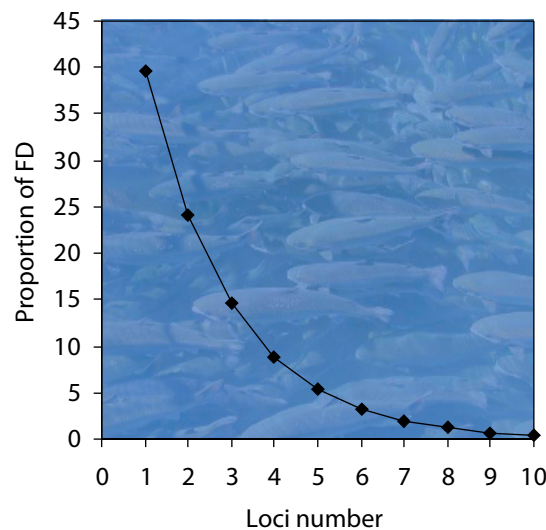
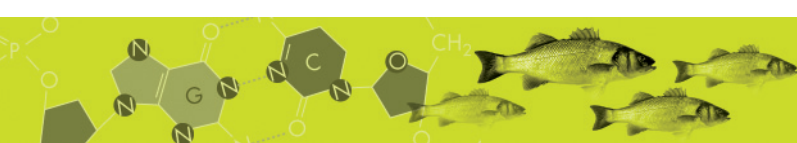


Fig. 5. Distribution of Fitness Differentials across loci (total FD sums to 100%).

The basic genetic model used was based on three sets of 10 unlinked loci, having an exponential distribution of Fitness Differentials (FD; i.e. the difference between a wild and cultured fish) (Fig. 5). Each set of 10 loci influences the fish in one of the three main life-history stages; embryonic, freshwater or marine/adult (see Fig. 4). The influence of genotype on phenotype is based on the interaction of empirically measured FDs and individual genotypes. Pure wild fish are defined as w/w homozygotes at all loci. Pure farmed fish are defined as f/f homozygotes at all loci, and it is these f alleles which are associated with the FD's calculated at each loci. Pure wild fish do not possess any f alleles, their total FD will thus sum to 0, and therefore they do not experience any change in the various population parameters (growth, survival, fecundity etc) associated with non-native inputs. Thus, the population parameters associated with pure wild fish remain those in the original wild population model. Pure farmed fish are f/f at all loci, and therefore the total sum of FD's over all loci for these fish will be 100. Individual fish with this genotype will therefore experience 100% of the empirically measured changes to the



various population parameters that have been found to be associated with farmed fish compared to wild.

Hybrid fish will have their total FD's calculated in the same way. F1 fish are w/f heterozygotes at all loci. Their total FD will therefore be the sum of single allele effects (i.e. $\frac{1}{2}$ of the full loci effect) at each loci. For these cross types this will sum to 50 and these fish will thus experience 50% of the FD associated with the various population parameters. Other hybrids will have varying proportions of f alleles. Each f allele will have a FD defined as $\frac{1}{2}$ the total effect at a particular loci, and the total FD for a fish will be the sum of each of these individual allelic effects. This, in turn, will define the proportion of the empirically measured changes to the various population parameters defined by the FD's that will influence the individual fish.

This novel genetic model has been developed to avoid some of the problems associated with previous 'mixing-models', where modeled behavior is based on the 'percentage hybridity' of an individual. Theoretical and empirical investigations (21, 22) have shown that the distribution of effects of fitness traits follows an exponential pattern. Thus, a 50% hybrid fish (F1) will experience significantly different fitness effects depending on the actual alleles it possesses, rather than just the hybrid generation it originates from. This basic model could be included in any future interaction models of new species, and as development has already been undertaken, could save significant time in the production of such models, whilst at the same time being more realistic than current genetic components.

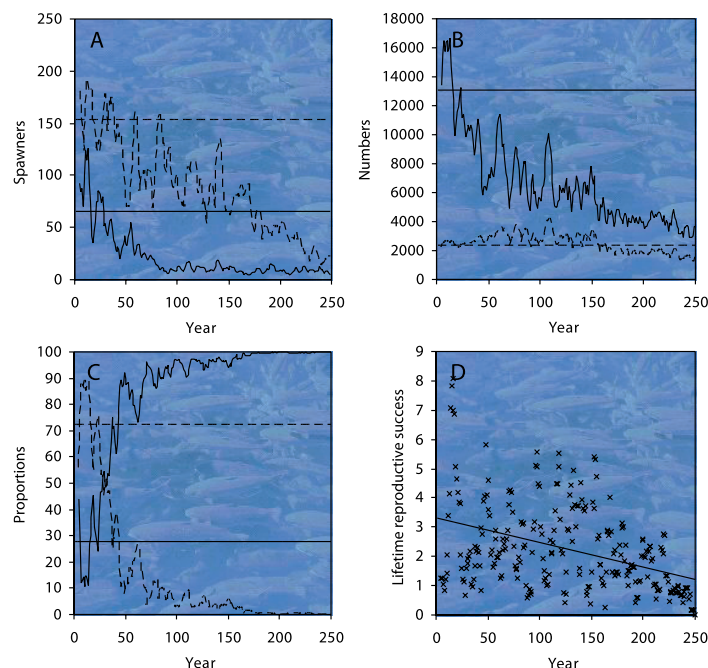


Fig. 6. Example salmon model partial outputs (19). A) Comparison of adult spawner numbers with 50 ± 5 non-native inputs per year into the wild population at mean ocean survival of 6% (dashed line) and 3% (solid line). Horizontal lines represent mean modelled spawner numbers with no non-native inputs at 6% (dashed line) and 3% (solid line). B) yearly parr (solid line) and smolt (dashed line) numbers. Horizontal lines represent mean modelled parr (solid line) and smolt (dashed line) numbers with no non-native inputs. C) proportions of 3+ (solid line) and 2+ smolts (dashed line). Horizontal lines represent mean modelled smolt proportions, with no non-native inputs, of 3+ smolts (dashed line) and 2+ smolts (solid line). D) Lifetime reproductive success of female spawners excluding that years non-native inputs. Note, all measures are 5 year running means and B, C and D are at a mean ocean survival of 3%.

Framework for developing modelling of cultured-wild interactions

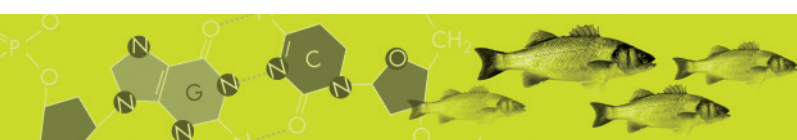
Modelling studies performed with the Atlantic salmon provide the basis for identifying a basic systematic approach to the development of interaction models for other species. In addition to the need to encompass both demographic and genetic processes, the approach involves the following basic steps:

- 1) collecting from literature life-history, demographic and genetic information on key processes and parameters, including data on demographical, behavioral, and fitness differences between wild and escaped cultured individuals
- 2) building basic conceptual model including both demographic and genetic components
- 3) programming integrated demographic and genetic model
- 4) setting of realistic demographic, genetic and fitness parameters model
- 5) corroborating demographic and genetic components of the model by comparing outputs with empirical data and assessing effect of different model settings and structures
- 6) running of simulations across range of interaction situations, or for specific scenarios of interest.

Taking a systematic approach to the development of interaction models ensures knowledge gaps to be identified at each stage. Corroboration of the model is essential to give confidence in model predictions so that results of simulations of interaction scenarios provide a scientifically supportable basis for management decisions to be made. Using the modeling approach, information from existing empirical studies can be generalized, and the need for more, expensive and time consuming experiments minimized, and future research priorities defined more clearly and precisely.

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