An Ecological-Economic Model on the Effects of Interactions between Escaped Farmed and Wild Salmon (*Salmo salar*)

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Running title: Economics of genetic effects of escapees on wild salmon

Abstract

This paper explores the ecological and economic impacts of interactions between escaped farmed and wild Atlantic salmon (*Salmo salar*, Salmonidae) over generations. An age- and stage-structured bioeconomic model is developed. The biological part of the model includes age-specific life history traits such as survival rates, fecundity, and spawning successes for wild and escaped farmed salmon, as well as their hybrids, while the economic part takes account of use and non-use values of fish stock. The model is simulated under three scenarios using data from the Atlantic salmon fishery and salmon farming in Norway. The social welfare are derived from harvest and wild salmon while the economic benefits of fishing comprise both sea and river fisheries. The results reveal that the wild salmon stock is gradually replaced by salmon with farmed origin, while the total social welfare and economic benefit decline, although not at the same rate as the wild salmon stock.

Keywords: age- and stage-structured model, genetic interaction, escaped farmed salmon, wild salmon, social welfare, economic benefit

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Introduction

Norway has around 450 rivers sustaining salmon and holds the world's largest spawning population for Atlantic salmon (*Salmo salar*, Salmonidae). Currently, about 40% of the overall catch in the North Atlantic are from Norwegian coastal waters and rivers (NASCO 2009). Wild salmon populations have suffered a steady decline in abundance in the last three decades. This decline is likely caused by a combination of factors associated with human activities including overexploitation, habitat degradation, salmon aquaculture, as well as changes in natural environment (e.g., Jonsson and Jonsson 2006; Hindar *et al*. 2006). Norway is the world's number one producer of farmed salmon with a total first hand value of almost NOK 20 billion in 2009 (Statistics Norway 2010). Concurrently, salmon aquaculture has developed rapidly from a few 1000 tons in 1980 to 1 million tons in 2010 (Statistics Norway 2010).

The rapid development of salmon aquaculture has raised concerns over ecological and environmental impacts on wild salmon populations and fisheries, particularly genetic interactions between escaped farmed and wild salmon and transmission of sea lice and other disease agents between farmed and wild fish. Each year, farmed salmon escape in large numbers from the net-pens, and enter rivers upon sexual maturation. Fiske *et al*. (2006) indicated that there is a significant positive correlation between the number of farmed escapees in rivers and the intensity of farmed salmon in the net-pens. It is estimated that escaped farmed salmon comprise on average 14 - 36% of the total spawning populations in Norwegian rivers, even up to 80% of the spawning populations in some rivers (Fiske *et al*. 2001; Hansen 2006). Escaped farmed salmon are able to leave offspring in the wild and interbreed with wild salmon (Fleming *et al.* 2000).

Farmed salmon were originally derived from wild salmon populations and have been artificially selected for economic traits such as growth rate, age at sexual maturity and resistance to diseases since the 1970s (Gjøen and Bentsen 1997). They are reared in controlled captive facilities with abundant food supply and few predation threats. Their genetic variability and some biological and behavior characteristics of farmed salmon have altered over time. Ultimately, farmed salmon are becoming increasingly genetically different from their wild counterparts (Weir and Grant 2005; Karlsson *et al*. in press).

Interbreeding between escaped farmed and wild salmon causes genotypic and gene expression changes in wild salmon populations (Roberge *et al*. 2008). It may also cause depression in the fitness and productivity of wild salmon (Hindar *et al.* 2006; Jonsson and Jonsson 2006). The cumulative reduction in fitness and productivity resulting from the repeated intrusion of escapees may, therefore, lead to severe declines in the salmon populations, and in a worst case scenario even wipe out the more vulnerable ones (Hurtchings 1991; McGinnity *et al*. 2003). Consequently, offspring from escaped farmed individuals may eventually replace the wild salmon populations (Hindar *et al.* 2006). The consequences of interbreeding can be exhibited in the changes in life history traits such as fecundity, breeding success, timing of spawning, age and size at smoltification, and stage specific survival and growth rates. Experiments in rivers and semi-natural stream channels (McGinnity *et al*. 2003; 2004; Fleming *et al.* 1996 & 2000) have shown that escaped farmed salmon and subsequent offspring are competitively and reproductively inferior to wild salmon, resulting in lower survival rates and reproductive success. A meta-analysis of existing global data also indicated that there are reductions in both survival and abundance in Atlantic salmon populations in association with increased production of farmed salmon (Ford and Myers 2008). In some rivers, offspring of farmed salmon attain larger body size and higher fecundity than their wild counterparts, but the increased egg production does not compensate for the reduced survival of escaped farmed salmon with respect to fitness (McGinnity *et al.* 2003). Hindar *et al*. (2006) developed a dynamic simulation model for Atlantic salmon which incorporated the changes in the fitness-related and phenotypic traits during interbreeding over generations, and further analyzed the genetic and ecological effects of escaped farmed salmon on wild salmon stocks with different intrusion rates.

While the ecological effects of genetic interactions between farmed escapees and wild salmon have been widely acknowledged, economic effects of such interactions have not been studied. This paper examines the combined ecological and economic impacts of genetic interactions between escaped farmed and wild salmon. Given different fishing mortalities, the productivity of wild salmon and the economic values from fishing and wild salmon population are analyzed by developing a dynamic bioeconomic simulation model. The biological component of the model describes the salmon population dynamics using an age- and stage-structured model that incorporates interactions between escaped farmed and wild salmon through relative differences in age specific life-history traits such as maturation rates, fecundity, spawning success, survival and growth rates. The economic component of the model includes both use and non-use values by estimating the benefit of fishing and non-market value of fish stock through a social welfare function.

The rest of the paper is structured as follows: Section 2 describes the age- and stage-structured biological model, while the economic model is presented in Section 3. The model specification and data are described in Section 4 while Section 5 shows the results and discussion. Conclusions with some policy implications are given in Section 6.

The Age- and Stage-structured Population Dynamic Model

Atlantic salmon is an anadromous species, meaning it lives in both marine and freshwater environments and migrates upstream to spawn. Wild Norwegian salmon populations spend on average 2 - 5 years in freshwater, from hatching until becoming smolts and migrating towards the sea. The salmon feed and grow at sea for 1 - 3 years, before returning to their natal rivers when reaching maturity. Mature salmon (spawners) migrate to the rivers during the summer and autumn, and spawn in late autumn. The fertilized eggs spend the winter in the gravel before hatching in the following spring. Thus, the Atlantic salmon have a relative complex life history with several distinct stages.

Escaped farmed salmon may enter the fjords and rivers at different life stages. Our analysis gives special emphasis on those that escape at the post-smolt stage, considered as early escapees (hereafter called FE for Farm Early escapees), and those that escape at the adult stage (FL for Farm Late escapees). Some of these escapees enter the rivers and participate in the spawning.

Each river and stock has its own population dynamics with different life histories (Hutchings and Jones 1998). Here we parameterize an age- and stage-structured model for an example river similar to River Imsa which is located in the southern part of Norway and has been subject to several studies (see Section 4), although with larger rearing environment and twice the recruitment. Simulations resulting from this model illustrate the effect of genetic interactions between farmed escapees and wild salmon, with an emphasis on the early life stages crucial for population regulation. The biological model framework is a modified form of the dynamic population model developed by Hindar *et al.* (2006), explicitly including a density-dependent stock-recruitment model. We assume that the Atlantic salmon life cycle is divided into five stages; from spawned eggs to hatching, to fry (recruitment), smolt, marine growth and finally returning to the next spawning. The wild salmon population is defined by the number of salmon at each age and stage. The dynamic age-stage-structured population models are captured in the equations below, while Figure 1 presents a schematic overview of a single cohort salmon population with inclusion of escaped farmed salmon.

Insert Figure 1 here

The spawning population will, for our example river, be made up of two age classes with different size distributions; salmon that have been one winter at sea (1SW, also called grilse) and those that have been two winters at sea (2SW). Some salmon populations also have a small number of older spawners but we choose to ignore these in our simulations. Another simplification is that we do not include repeated spawners, although as many as 10 % of female spawners may spawn twice (Mills 1989). When modelling the spawning, we assign the spawners to five categories (Hindar *et al.* 2006): wild (W), hybrid offspring with wild and escaped farmed salmon as parents (H), offspring from escaped farmed salmon (F), and then the spawners that themselves have escaped as post-smolts (FE) or as adults (FL). We will in this simulation assume that all age classes and categories have an equal sex distribution. In addition, some of the male parr also mature in freshwater and participate in the spawning; wild parr (WP), hybrid parr (HP) and feralized farm offspring parr (FP).

According to sex and category, each spawner is assigned a spawning success rate (Table 1; Hindar *et al.* 2006) where the spawners that have spent their life roaming freely (W, H and F) have the best success and the late escapees (FL) are the least successful, i.e. they are the least fit for the competition on the spawning grounds. By introducing average weights for the females of each age and category, and applying a general fecundity weight relationship (Hindar *et al.* 2011), we are able to generate the size and composition of the fertilized egg pool. The eggs are then assigned to one of six categories; just wild parents (W), hybrids with one wild and one farmed parent (H), just farmed parents (F), back-cross of hybrid to wild, i.e. with one hybrid and one wild parent (BCW), back-cross to farm (BCF), and finally second or later generation hybrids (2GH).

After hatching and swim-up the following spring, the recruitment to the fry stage in their first autumn ("0+") is described by a Shepherd Stock-Recruitment (SR) model (Shepherd 1982). Our modified Shepherd SR-function is defined as:

(1) $$R_{i,t} = \frac{a_i S_{i,t}}{1 + \left(b S_{tot,t}\right)^{\beta}},$$

where $S_{i,t}$ is the spawning stock, measured as the number of fertilized eggs, of category i spawned in year t, $S_{tot,t}$ is the total spawning stock over all categories, and $R_{i,t}$ is the fry recruitment of category i from the same cohort. The parameter a_i is the gradient of the function when the stock $S_{i,t}$ approaches zero and represents the density independent survival from fertilized egg to fry for category i, b is the strength of the density-dependent regulation assumed equal for all categories, and the parameter β gives the curvature of the density dependence.

Further, we assume that all fish smoltify as 2 year old juveniles with a category specific survival rate $s_{1,i}$ from fry to smolt (see Table 1), so the number of smolt of category i from spawning cohort t becomes simply

(2) $$Sm_{i,t} = s_{1,i} R_{i,t} .$$

For the marine phase we just have available data on survival and maturation for the W, H and F categories, so to reduce the number of categories half of the back-crosses of hybrids to wild fish (BCW) are allocated to the W category and the other half to the H category. Similarly, half of the back-cross to farm category (BCF) is allocated to the F and the other half to the H category. The second generation hybrids are allocated entirely to the H category. As a result, the H category eventually consists of a diverse set of first and later generation hybrids, as well as half of the various backcrosses to wild and farmed fish. Furthermore, the W and F categories include proportions of the backcrosses, in addition to the fish of entirely wild and farmed pedigrees respectively.

From a cohort t, the number of returning 1SW spawners of a given category $N1_{i,t}$ depends on the survival rate the first year at sea $s_{1s,i}$ and the corresponding maturation rate μ for 1SW, giving the equation

(3) $$N1_{i,t} = Sm_{i,t} s_{1s,i} \mu .$$

By assuming all remaining salmon mature as 2SW, Equation (4) describes the number of returning 2SW spawners for a category i from the survival rate the second year at sea $s_{2s,i}$:

(4) $$N2_{i,t} = Sm_{i,t} s_{1s,i} (1-\mu) s_{2s,i} .$$

Finally, the returning mature 1SW and 2SW salmon experience harvesting both along the coast and in the rivers during their migration back to their native spawning grounds. The number of returning 1SW and 2SW surviving the combined sea and river fishing to spawn in a given year *t+4* then becomes

(5) $$X1_{i,t+4} = N1_{i,t}\left(1 - f_{1,t+4}\right) \text{ and}$$

(6) $$X2_{i,t+4} = N2_{i,t-1}\left(1 - f_{2,t+4}\right),$$

where $f_{1,t}$ and $f_{2,t}$ is the fishing mortality for 1SW and 2SW respectively, which may vary between years. However, in the next section, on the economic benefit modelling, we use $X_t = X1_t + X2_t$ for the total spawning stock.

The Economic Benefits

Returning salmon are first harvested by commercial, or semi commercial, fishermen in the fjords and inlets along the coast. The surviving individuals are then targeted by recreational anglers in the rivers. The commercial catch is destined for meat value, whereas recreational fishing is for sport and leisure, and possibly also personal consumption. Thus, the economic benefits to be measured here are based on sequential salmon harvests from sea and river. Besides fishing, or direct use values, wild salmon also has non-use values such as an intrinsic value (existence value), simply because of its existence in the environment. A special emphasis is therefore given to incorporate such non-use values (see e.g. Freeman 2003 for a general overview). Due to the above two-sided values derived from salmon, two different ways to measure these values are analysed in this paper. First, we consider the use value where the fishing monetary value of the salmon population is only taken into account. We next consider the conservation and use perspective where both the harvest and stock are included, and where the utility, or welfare, of the salmon is described in number of fish harvested and the size of the wild standing stock.

The economic benefit based on the direct use value only is measured by the market value of the total harvest. The benefit includes two parts: commercial fishing in the sea and recreational fishing in the river. The benefit from sea fishing is measured by meat value at market prices. Leaving the recently escaped farmed salmon out, it is assumed that the sea fishermen consider *fish is just a fish*, the prices thus only differ in fish size and associated weights, and are unaffected by salmon categories. On the contrary, the benefit from recreational fishing is generated through selling fishing permits which is measured by the anglers' willingness-to-pay (WTP) on the basis of the quality and quantity of wild salmon stock (Olaussen and Skonhoft 2008). An important quality factor taken into account here is the composition of the salmon stock; that is, the mix between wild and farmed salmon. Olaussen and Liu (2010) indicate that salmon anglers are willing to pay substantially more for the pure wild or 'clean' salmon stock. Therefore, the WTP is measured in response to the changes in the composition of wild salmon in the total spawning population of all three categories (more details below). Thus, the economic benefit over the evaluation period, comprising T years, is written as:

$$(7) \quad \Pi = \sum_{t=1}^{T} \rho^t \pi_t = \sum_{t=1}^{T} \rho^t [\sum_{j=1}^{2} (p^{s,j} Y_t^{s,j}) + p_t^r Y_t^r],$$

where $\rho^t = 1/(1+\omega)^t$ is the discount factor with a discount rate $\omega \geq 0$.

The first term in the square brackets on the right hand of this equation, $p^{s,j} Y_t^{s,j}$, describes the profits from sea fishing while the second term, $p_t^r Y_t^r$, represents the benefit from river fishing. The parameters $p^{s,j}$ are the net market prices for salmon harvested which include 1SW ($j=1$) and 2SW ($j=2$) salmon, assumed to be independent of harvest intensity, time, and categories, but related to age classes, and $Y_t^{s,j}$ are the catches of all three categories of salmon from 1SW and 2SW measured in wet weight (in kg), only separated by age classes. p_t^r is the price of salmon caught in the river (in NOK per kg) transformed from the fishing license fee that anglers are willing to pay. The price of a fishing license is determined by the composition of the wild salmon in the total returned spawning population (more details are provided in Section 4). For this reason, p_t^r generally changes over time. Finally, Y_t^r is the total harvest from river fishing in wet weight (in kg).

We next consider the conservation and use perspective of salmon by formulating a utility, or welfare, function. As indicated, it includes two components: the utility provided through harvesting salmon (use value) and the utility derived from the intrinsic value (non-use value) the wild salmon stock possesses. When assuming separability, the social welfare at time t is thus written as $W_t = \alpha[U(Y_t)] + (1-\alpha)[V(X_t^w)]$, where $U(Y_t)$ represents the utility from the harvested salmon while $V(X_t^w)$ is the utility from the wild spawning salmon stock, that is, the intrinsic value of the wild salmon stock.

Both $U(Y_t)$ and $V(X_t^w)$ are assumed to be increasing and concave functions, i.e., it is assumed that a higher salmon stock as well as a higher harvest yields a higher utility, but at a declining rate. $0 \le \alpha \le 1$ is a parameter weighting for the utility level of harvesting (see, e.g., Kurz 1968 for a similar treatment within a neoclassical economic growth framework). If $\alpha = 0$ it hence implies that only the size of the wild stock is taken into account; and if $\alpha = 1$ it means that only the harvesting counts while $\alpha = 0.5$ implies en equal valuation of the harvest and stock abundance. Y_t is the harvest including 2 classes: *1SW* and *2SW*, and three categories of salmon: wild (W), hybrid (H) and feral (F) from sea and river fishing. The stock, X_t^w, only refers to wild salmon where the two spawning classes, 1SW and 2SW in the sea and river are included. All the harvests and wild stock are measured by their respective average body weights in kg, which differ between age classes and salmon categories. The present value of welfare is hence described by:

(8) $$W = \sum_{t=1}^{T} \rho^t W_t = \sum_{t=1}^{T} \rho^t \{\alpha[U(Y_t)] + (1-\alpha)[V(X_t)]\},$$

where $\rho^t = 1/(1+\delta)^t$ is the utility discount factor with $\delta \geq 0$ as the discount rate.

Model Specification and Data

Based on the bioeconomic model developed above (Sections 2 and 3), we use an example river where the fitness parameters (Table 1) are similar to those obtained from the experiments in River Imsa in Norway (Fleming *et al.* 2000) and Burrishoole river system in Ireland (McGinnity *et al*. 2003) to illustrate the potential ecological and economic effects of interbreeding between farmed and wild salmon (following Hindar *et al.* 2006).

We specify the welfare function defined in Eq. (8) by letting both $U(Y_t)$ and $V(X_t^w)$ have a logarithmic form: $W_t = \alpha \log(Y_t) + (1-\alpha)\log(X_t^w)$. The one-day fishing license price is defined based on the salmon anglers' WTP study by Olaussen and Liu (2010). The survey was conducted among salmon anglers nationwide in 2005 and 2006 (Olaussen 2005; Olaussen and Liu 2010). The main findings from the survey were that for a one-day fishing license the salmon anglers are willing to pay NOK 242 if their catch was made of pure wild salmon, NOK 94 if the catch was half wild and half farmed salmon, while they only want to pay NOK 34 if the catch was completely made up of farmed salmon, *ceteris paribus*. Here we consider both escapees and their offspring as farmed, although most anglers will have problems differentiate between wild salmon and offspring from escapees. Based on these findings, a simple polynomial regression model is fitted. Let p_t^{r0} represent the price per one-day fishing license (NOK per day), then we have: $p_t^{r0} = 176k_t^2 + 32k_t + 34$, where $0 \le k \le 1$ is the proportion of wild salmon in the total spawning population at *t*. If $\overline{w}_r$ is the averaged weight of salmon caught in rivers per day or per fishing license period (in kg/day), then the price of salmon caught in rivers writes: $p_t^r = p_t^{r0} / \overline{w}_r$ (in NOK per kg).

The model is run for a period of 40 years, $T = 40$, that is, about 10 salmon generations for the modelled salmon populations. To get realistic initial numbers for 1SW and 2SW spawners , we first run the age structured model for 100 years, based on the parameters of other life-history traits such as fecundity, spawning success rate, and age specific survival rates, but without any fishing mortality or escapees. After this burn-in period, the wild salmon population will arrive at an equilibrium state where the size of the population remains at a constant level. We then use these equilibrium values for 1SW and 2SW wild salmon spawners as initial values at year 1 (see horizontal blue lines, marked as "Unfished", in Figures 2. Provided that the salmon population is also affected by other factors, such as habitat characteristics and climate factors, using unfished (virgin) stock size may solely concentrate on the escape problem, *ceteris paribus*.

A large number of parameter values is required to run the simulation model (Table 1). Some are extracted from the other studies, some are estimated based on the collected field data and some are calibrated from general fishing practice in Norway. These parameter values with references are reported in Table 1. The most important variable for our paper is the number of escapees in the spawning population in a river. The number of farmed salmon escapees from net-pens depends on farmed production and onsite management (Fiske *et al.* 2006) whereas the proportions farmed escapees which make up in the spawning populations also depend on the size of the wild stock. The monitoring program for Norwegian wild salmon revealed that on average 20% of the spawning population is of farm origin, although the number of escaped salmon varies from year to year (Fiske *et al*. 2001; Hansen 2006; Hindar *et al*. 2006). Additionally, as we use the equilibrium (unfished) population at year 1, a fixed number of escapees which is 20% of the equilibrium spawning population at year 1 will enter the spawning population annually. Therefore, in order to have a comprehensive understanding how farmed escapees affect wild salmon populations and fisheries, the simulation model is run under three scenarios for farmed escapees: Scenario I) without escapees; Scenario II) escapees constitute 20% of the annual spawning population from year 1; Scenario III) with a constant number (50) of escapees entering the river each year from year 1. Moreover, we also use discount rates equal to zero when estimating economic benefits and welfare, i.e., in our simulations we set $\delta = 0$ and $\omega = 0$. This is because wild salmon population should be managed in a sustainable manner, indicating that future generations should have the same possibility to experience wild salmon as the present generation (NOU 1999). Three values for weighting the utility value of harvesting α are used: 0, 0.5, and 1 in the welfare function (Eq. 8). Fishing mortalities ranging from 0 to 0.9 are applied in the simulations.

The fishing mortality rates for different fishing environments and age classes have to be specified before running simulations. In the sea fishing there is a size bias in the harvest so that it is more likely to catch a large salmon than a smaller one (Strand and Heggberget 1996), whereas in the river fishing the size bias is reversed; now it is less likely to catch the larger salmon. Strand and Heggberget (1996) only investigated the size bias for wild salmon but we assume this effect applies for all three categories of salmon, i.e. wild, hybrid and feral. First, we assume that the combined sea and river fishing mortality rates for both age classes are approximately equal. The annual combined fishing mortality will change slightly through the simulation period of 40 years due to changes in the age distribution, caused by the increase in farm offspring spawners. The different levels of fishing mortality rates applied in the simulations will be referred to by the rate for a population with equally many spawners of both age classes. The same fishing mortality rate is then applied annually for the 40 simulated years. Thus, the fishing mortalities presented in tables and figures in next section are the averaged numbers over 40 years. The simulations are conducted using the statistical software R (R Development, Core Team 2009).

Insert Table 1 here

Results and Discussions

Scenario I - Without escapees

This scenario with no escaped farmed salmon entering the river is illustrated in Figure 2 and will be used as a benchmark for the other scenarios (Scenarios II and III). Therefore, fishing is assumed to be the only manmade factor affecting the salmon population in this scenario. Given a fishing mortality larger than 0, the spawning population will gradually decline, and reach an equilibrium state or steady state after some years (Figure 2). An increased fishing mortality rate will result in a faster decline in salmon population. The maximum harvest (in kg) over 40 years is achieved at a fishing mortality of 0.8, where the fish stock reaches a stable state after about 10-12 years (top panel in Table 2). These results are similar to those found in Hindar *et al.* (2011) and depend on the strength of natural mortality.

Insert Figure 2 and Table 2 here

The direct economic benefits from sea and river fishing, Π, as described by Eq. (7) are reported in Table 3 (upper part). The highest economic benefit is obtained with a fishing mortality of 0.7 for river fishing, and 0.8 for sea fishing. This difference in fishing mortality is observed because sea fishing harvests a higher proportion of 2SW than 1SW fish while river fishing catches proportionally more 1SW fish, and because 2SW fish is twice heavier than 1SW fish. The overall economic benefit is highest at the fishing mortality of 0.7, as river fishing yields substantially higher benefit than sea fishing because the anglers' willingness-to-pay for a fishing license in rivers is much higher than the meat values received from sea fishing (see also Section 3). The social welfare, W, described by Eq. (8) varies with different fishing mortalities and weights for the utility level of harvesting α (top panel in Table 4). The highest welfare ($W = 112.52$) is achieved when there is no fishing ($f = 0$) and only stock size counts ($\alpha = 0$).

Insert Table 3 and 4 here

Scenario II - Escapees constitute 20% of the total annual spawning population

Figures 3, 4 and 5 present the spawning population, total harvest and economic benefits respectively when the escapees constitute 20% of annual spawning population. For all fishing mortalities, the biomass of wild salmon declines (downward curves, Figure 3) while the biomass of farmed salmon increases (upward curves, Figure 3), although the magnitude of those changes increase with higher fishing mortality. In the case of no fishing, the spawning population has lost roughly 54% of its wild biomass, but has gained 40% of salmon of farmed origin from year 1 to year 40 after about 10 generations. The total biomass of spawning population is reduced by 7% due to effects of interbreeding because hybrid and feral salmon have lower lifetime fitness, but are heavier than wild salmon. However, in terms of numbers, the reduction in the wild spawners and total spawning population is more severe, respectively representing 77% and 26% of losses, and the salmon of farmed origin has become dominant genotype of the spawning population.

The decline in stock size will naturally become steeper when fishing takes place. For example, with an annual total fishing mortality of 0.70, the wild spawning stock is reduced by 84%, while the total spawning stock loses 73% over 40 years. The salmon that are partially or fully of farmed origin constitute 75% of the total spawning stock at year 40. Likewise, the wild salmon stock loses almost 94% of its original size with a fishing mortality of 0.9. This may suggest that the wild salmon stock is at the edge of collapse, if not collapsed yet, biologically. These findings are similar to those found in Hindar *et al*. (2006).

Insert Figure 3 here

The total harvest from both sea and river fishing declines for the first 8 years (two generations), especially so for the simulations with the higher fishing mortalities. After this initial period, the harvest remains relatively stable except for the fishing mortality of 0.9 where the harvest continues to decrease for the whole simulation period. However, the higher fishing mortality yields greater harvest at the first generation, but the total harvest is the highest for fishing mortalities 0.8 (Figure 4, and middle panel in Table 2). The economic benefit of sea and river fishing follows the same trends as the harvest. Compared to Scenario I without escapees, the economic benefits from sea fishing have dropped slightly, whereas the economic benefits from river fishing has been reduced considerably given the same fishing mortality. The reason for this difference between sea and river economic benefits is, as already indicated, that sea fishermen consider *a fish as a fish* no matter if it is wild or farmed. Therefore, the drop in the number of wild fish is compensated by the weight gained from the larger hybrid and feral fish. On the other hand, anglers are willing to pay substantially more for fishing wild salmon. However, the economic benefit of river fishing is still much larger than that of sea fishing. The economic benefit over the simulation period is first improved when the fishing mortality is increased, then reaches its maximum at a fishing mortality of 0.8, and is then reduced again for a fishing mortality of 0.9 (Figure 5; middle panel in Table 3). The maximum social welfare value of 100.42 is obtained for a fishing mortality of 0.7 and a weight for the utility level of harvesting $\alpha = 1$. This maximum social welfare value is lower than that found for Scenario I, i.e. with no escapees where the maximum social welfare value of 112.52 is achieved for no fishing and $\alpha = 0$. Moreover, for given any fishing mortalities and values of α, the social welfare is always lower under Scenario II than in Scenario I with no escapees (middle panel in Table 4).

Insert Figures 4 and 5 here

Scenario III - With escapees – 50 escapees each year

The third scenario assumes that a fixed number of escapees (50) enter the spawning stock each year. When the fishing mortality is increased, leading to a decrease in the number of remaining spawners, a fixed number of annual escapees will account for an increasing proportion of the total spawning population. The change in the composition of spawning population will thereby be more dramatic than in Scenario II. For instance, with a fishing mortality of 0.5 or higher the last wild salmon will have disappeared before 40 years, suggesting that salmon of full or partial farm origin have completely replaced the wild stock (Figure 6). In contrast, the total harvest increases with higher fishing mortality due to the high annual addition of escapees. Thus, the maximum annual harvest is obtained for a fishing mortality of 0.9 (Figure 7). The consequences for the economic benefit of increasing the fishing mortality under Scenario III are, however, not unambiguous. The economic benefit from sea fishing keeps rising with increasing fishing mortality, while the economic benefit from river fishing reaches its highest value over the 40 year period for a fishing mortality of 0.6 (bottom panel in Table 3 and Figure 8). After 40 years, the wild salmon stock has vanished for all fishing mortalities higher than 0.25. The total economic benefit is improved with a progressively higher fishing mortality. The economic benefit of sea fishing for fishing mortalities of 0.5 or more is the highest among the three scenarios (bottom panel in Table 3), because we under Scenario III annually add most new escapees to the population among three scenarios. A fixed number of 50 escapees account for 20% of the total spawning stock in the first years, then gradually becomes a larger proportion to the total spawning stock as the number of returning spawners is declining. Finally, the spawning population will consist of salmon of farmed origin only. In other words, the exploitable population is becoming bigger through time. Similarly, the highest social welfare value is obtained for a fishing mortality of 0.9. These results indicate that a high proportion of escapees will enhance the total harvesting population for the higher fishing mortalities, and consequently yield higher catch levels and economic benefits if offspring from farmed salmon are perceived as and valued as wild salmon like the case of sea fishing.

Insert Figures 6 and 7 here

For any given fishing mortality and α value, the social welfare will be lower when there are escapees in the spawning population, compared to Scenario I without any escaped farmed salmon. The larger the proportion of escapees in the spawning population is, the smaller will the social welfare value become (Table 4). However, the difference in social welfare between the scenarios is decreasing for increasing values of α, because we go from $\alpha = 0$, where only the size of the wild stock is valued, then to $\alpha = 0.5$ where the harvest and stock values are equally weighted, finally to $\alpha = 1$, where only the harvest matters. Although

α is an exogenous variable in welfare analysis (Eq. 8), these results, however, suggest that when conservation of wild salmon population is the dominant management strategy, lower fishing mortality rates are required. When the socioeconomic benefit for society is the main concern, higher fishing mortality will be necessary. If conservation and socioeconomic objectives are equally weighted, an intermediate fishing mortality (~ 0.5) will be the most favourable.

Finally, both the sea harvest and the economic benefit of sea fishing are reduced with decreasing proportions of escapees in the spawning stock. The economic benefit of river fishing will, on the other hand, increase when the proportion of escapees is reduced due to the assumption that fishermen and anglers value offspring from farmed salmon differently.

Insert Figure 8 here

Conclusions

This paper has developed a bioeconomic model that describes the impacts of genetic interactions between wild and escaped farmed salmon. The ecological and economic effects of farmed escapees on wild salmon populations and fisheries are illustrated by simulations from the model, based on fitness parameter estimates similar to those from River Imsa in Norway. Simulations from three scenarios, without or with escapees, are conducted with a range of fishing mortalities. This study is, to our knowledge, the first numerical analysis carried out in the level of population dynamics to investigate the economic impacts of genetic interaction between escapees and native species, or genetic 'pollution' from farmed escapees to native species. The model has explicitly included stage specific life-history traits, and use and non-use values of salmon stock. Guttormsen *et al.* (2008, see also some references mentioned in the paper) described a theoretical framework of optimal harvest of genetically different populations.

The results indicate that the composition of the spawning population will change dramatically when escaped farmed salmon are participating in the spawning over a 40 year period, i.e. about 10 salmon generations. The number of wild salmon declines while the number of farmed offspring will increase. The trends get stronger with higher escape rates and eventually the salmon with farmed origin will dominate the spawning population, and even replace the wild stock completely, if the invasion of escapees is large enough. This was the case for Scenario III, where the number of new escapees was the same each year, regardless of how large the wild or feralized spawning population was.

The economic benefits were also affected by the genetic interactions between wild and farm offspring. For a given fishing mortality, the total economic benefit will decrease with increasing proportions of escaped farmed salmon in the spawning population. If the economic benefit is split between sea and river fishing, we see the same trend for the economic benefit of river fishing, i.e. it is decreasing when the proportion of farmed offspring in the population is increasing. For sea fishing we see the opposite result; for a fishing mortality above 0.5 the economic benefit will grow when the proportion of escapees increase because the harvestable population will also increase and the market price is the same for wild salmon and farmed offspring. However, if the offspring from escaped farmed salmon is perceived to have a lower market value than wild ones, the economic value for the sea fishing may also decrease with increasing proportion of escapees, although the total harvest may become larger. Moreover, if the wild stock value (such as intrinsic value) is taken into account, further losses will be observed when the proportion of escapees increases. In a long term perspective, conserving the wild salmon stock by reducing the number of escapees and only allowing a modest fishing mortality will give a higher benefit for society. However, it becomes clear that the genetic effects of farmed escapees on wild salmon stock are severe, even devastating whereas the economic consequences are ambiguous.

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Table 1. The parameter values for the bioeconomic model.

Parameters	Values	Source
Fecundity ratio (eggs/kg)	1450	Hindar *et al*. 2011
Female spawning success rate		
Wild	0.90	Hindar *et al*. 2006
Hybrid	0.90	Hindar *et al*. 2006
Feral	0.90	Hindar *et al*. 2006
Farmed_early	0.82	Hindar *et al*. 2006; Fleming *et al*. 1997
Farmed_late	0.40	Hindar *et al*. 2006; Fleming *et al*. 1996 &2000;
Adult male relatively spawning success rate		
Wild	1.00	Hindar *et al*. 2006
Hybrid	1.00	Hindar *et al*. 2006
Feral	1.00	Hindar *et al*. 2006
Farmed_early	0.51	Hindar *et al*. 2006
Farmed_late	0.13	Fleming *et al*. 1996 &2000;
Male parr maturity rate at age 0+		
Wild	0.18	Fleming *et al*. 2000
Hybrid	0.13	Fleming *et al*. 2000
Feral	0.14	Fleming *et al*. 2000
Male parr relative spawning success rate		
Wild	1.00	Garant *et al*. 2003; Weir *et al*. 2005;
Hybrid	2,.33	Garant *et al*. 2003; Weir *et al*. 2005;
Feral	1.89	Garant *et al*. 2003; Weir *et al*. 2005;
Proportion of eggs sired by male parr	0.235	Garant *et al*. 2003; Weir *et al*. 2005;
Stock-Recrecuitment model parameters		
a	0.171	Estimated from Imsa river
b (#/m2)	0.271	Estimated from Imsa river
Beta	0.961	Estimated from Imsa river
Area (m2)	94100	Estimated from Imsa river
Maximum density independent survival rate of from swim-up to 0^+		
Wild	0.17	Estimated from Imsa river; McGinnity 1997;
Hybrid	0.11	Estimated from Imsa river; McGinnity *et al*. 2003;
Feral	0.15	Estimated from Imsa river; McGinnity 1997; McGinnity *et al*. 2003;
BCW	0.14	Estimated from Imsa river; McGinnity 1997; McGinnity *et al*. 2003;
BCF	0.12	Estimated from Imsa river; McGinnity 1997; McGinnity *et al*. 2003;
2GH	0.13	Estimated from Imsa river; McGinnity 1997; McGinnity *et al*. 2003;

Survival rate from age 0+ to 2+ old smolt		
Wild	0.25	Fleming *et al*. 2000; McGinnity 2003; Hindar *et al*. 2006;
Hybrid	0.23	Fleming *et al*. 2000; McGinnity 2003; Hindar *et al*. 2006;
Feral	0.27	Fleming *et al*. 2000; McGinnity 2003; Hindar *et al*. 2006;
BCW	0.28	Fleming *et al*. 2000; McGinnity 2003; Hindar *et al*. 2006;
BCF	0.28	Fleming *et al*. 2000; McGinnity 2003; Hindar *et al*. 2006;
F2	0.33	Fleming *et al*. 2000; McGinnity 2003; Hindar *et al*. 2006;
Survival rate from smolt to 1SW		
Wild	0.10	Hindar *et al*. 2006; Estimated from Imsa river
Hybrid	0.09	Hindar *et al*. 2006; Estimated from Imsa river
Feral	0.06	Hindar *et al*. 2006; Estimated from Imsa river
Survival rate from 1SW to 2SW		
Wild	0.50	Calibrated
Hybrid	0.50	Calibrated
Feral	0.50	Calibrated
Maturity rate in 1SW		
Wild	0.67	Calibrated
Hybrid	0.57	Calibrated
Feral	0.00	Calibrated
Fishing		
Averaged weight of salmon caught per day in rivers (kg/day)	0.50	Statistics Norway
Weight		
1SW wild (kg)	2.00	Calibrated
1SW hybrid (kg)	2.40	Calibrated
1SW Farmed (kg)	2.80	Calibrated
2SW wild (kg)	5.00	Calibrated
2SW hybrid (kg)	6.00	Calibrated
2SW farmed (kg)	7.00	Calibrated
Salmon prices		
1SW in the sea (NOK/kg)	40	Calibrated
1SW in the sea (NOK/kg)	60	Calibrated

Table 2. Harvest (‘000kg) from sea and river fishing under different fishing mortalities over 40 years. Highlights show the maximum harvest value.

Fishing mortality	0.25	0.4	0.5	0.6	0.7	0.8	0.9
Scenario I - without escapees							
Sea fishing	2.86	4.78	5.61	7.14	8.17	**8.84**	8.49
River fishing	2.87	4.05	4.92	5.40	**5.72**	5.49	4.40
Total benefit	5.73	8.84	10.53	12.54	13.89	**14.33**	12.89
Scenario II – with escapees (20%)							
Sea fishing	2.73	4.53	5.52	6.85	7.92	**8.53**	8.20
River fishing	2.67	3.74	4.37	4.90	**5.10**	5.01	4.15
Total benefit	5.40	8.27	9.89	11.85	13.02	**13.54**	12.35
Scenario III – with escapees(50)							
Sea fishing	2.74	4.50	5.54	7.03	8.40	9.79	**11.58**
River fishing	2.48	3.56	4.06	**4.42**	4.41	4.18	3.50
Total benefit	5.22	8.06	9.60	11.45	12.81	14.97	**15.08**

Table 3. Economic benefits ('000 NOK) from sea and river fishing under different fishing mortalities over 40 years. Highlights show the maximum economic benefits.

Fishing mortality	0.25	0.40	0.50	0.60	0.70	0.80	0.90
Scenario I - without escapees							
Sea fishing	174	287	334	426	487	**527**	507
River fishing	1390	1961	2380	2615	**2770**	2656	2129
Total benefit	1564	2248	2714	3041	**3257**	3183	2636
Scenario II – with escapees (20%)							
Sea fishing	170	276	337	418	483	**520**	499
River fishing	714	1007	1183	1344	1421	**1421**	1227
Total benefit	884	1283	1520	1762	1904	**1941**	1726
Scenario III – with escapees(50)							
Sea fishing	171	280	346	445	541	639	**773**
River fishing	551	734	807	**834**	815	770	655
Total benefit	722	1010	1153	1279	1356	1409	**1428**

Table 4. Social welfare from harvesting and wild salmon stock with different α values and fishing mortalities under three scenarios over 40 years ($\alpha = 0$ only stock value; $\alpha = 1$ only harvest value). Highlights show the maximum value given a weight of α.

Fishing mortality \ Weight α	0.0	0.5	1.0	0.0	0.5	1.0	0.0	0.5	1.0
	Scenario I (no escapees)			*Scenario II (20%)*			*Scenario III (50)*		
0.00	**112.52**	56.26	0.00	**99.95**	49.98	0.00	**97.58**	48.79	0.00
0.25	107.45	96.85	86.24	94.91	90.05	85.19	86.62	**85.56**	84.50
0.4	103.70	98.73	93.76	91.12	91.85	92.59	76.85	84.48	92.11
0.5	100.86	**98.83**	96.79	88.40	**92.04**	95.68	68.22	81.67	95.12
0.6	96.41	98.12	99.83	83.96	91.32	98.68	53.72	75.49	98.16
0.7	91.04	96.31	101.58	78.66	89.54	**100.42**	40.72	70.41	100.10
0.8	84.37	93.21	**102.05**	71.96	86.49	100.01	31.04	66.30	101.56
0.9	71.84	85.86	99.88	59.50	79.27	99.03	21.09	61.99	**102.89**

Figure 1. Schematic representation of the Atlantic salmon life cycle, with the addition of escaped farmed salmon into the spawning population. The illustrated stages are fertilized eggs E; fry (0^{+}) recruitment R; the number of smolts N_s; adult marine stages including 1 sea-winter N_{1sw} and 2 sea-winter N_{2sw} salmon; early farmed escapees, Y_1; and late farmed escapees, Y_2. Fishing takes place during the migration towards their native spawning grounds. $s_{(\cdot)}$ is an age-specific survival rate; θ is the fraction of mature male parr participating in the spawning; μ is the fraction of 1 sea-winter salmon maturing and returning towards the river; and f_1 and f_2 are the fishing mortality rates for1 and 2 sea-winter salmon respectively.

Figure 2. Spawning populations of wild salmon in weight (a) and total harvest in weight (b) for Scenario I without escapees. The simulations are run under different fishing mortalities.

Figure 3. Spawning stocks of wild (W) and farmed (F, including feral and hybrid) salmon for Scenario II, with 20% escapees entering the spawning population each year. The simulations are run with different fishing mortalities.

Figure 4. Total harvest (in kg) for Scenario II, with 20% escapees entering the spawning population each year. The simulations are run with different fishing mortalities.

Figure 5. Economic benefits of sea fishing (a) and river fishing (b) for Scenario II, with 20% escapees entering the spawning population each year. The simulations are run with different fishing mortalities.

Figure 6. Spawning stocks of wild (W) and farmed (F) salmon for Scenario III with a fixed number of escapees (50) entering the spawning population each year. The simulations are run with different fishing mortalities.

Figure 7. Total harvest for Scenario III with a fixed number of escapees (50) in weight under different fishing mortalities

Figure 8. Economic benefits of sea fishing (a) and river fishing (b) for Scenario III with a fixed escapees (50) under different fishing mortalities.

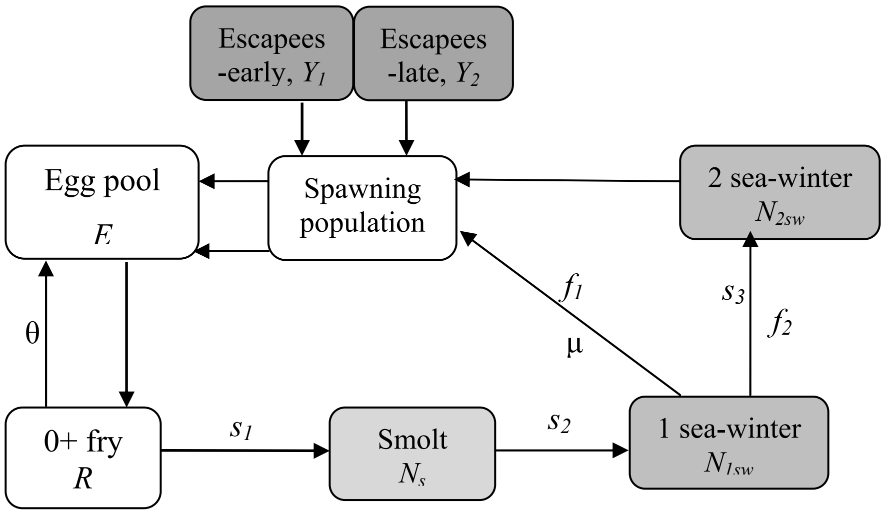

Escapees
-early, Y_1
Escapees
-late, Y_2
Egg pool
E
Spawning
population
2 sea-winter
N_{2sw}
θ
f_1
μ
s_3
f_2
0+ fry
R
s_1
Smolt
N_s
s_2
1 sea-winter
N_{1sw}

Figure 1.

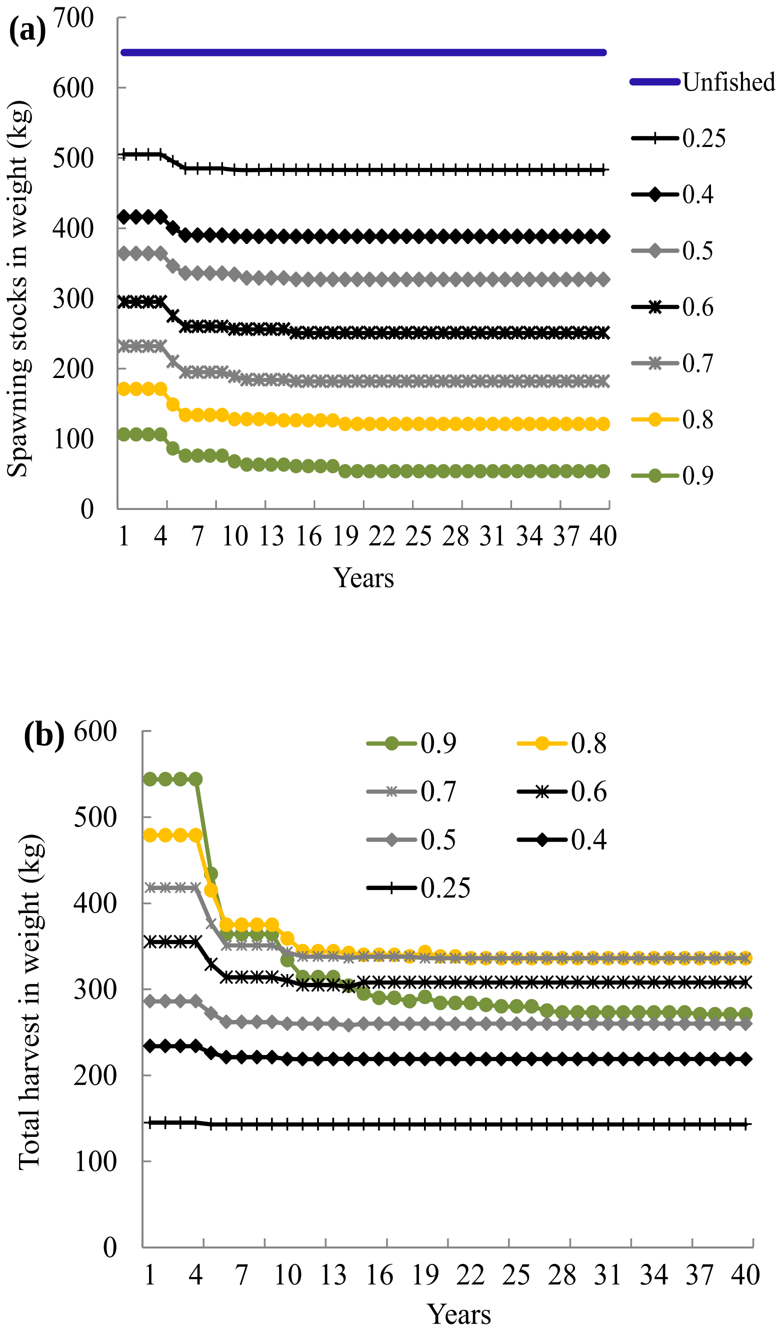
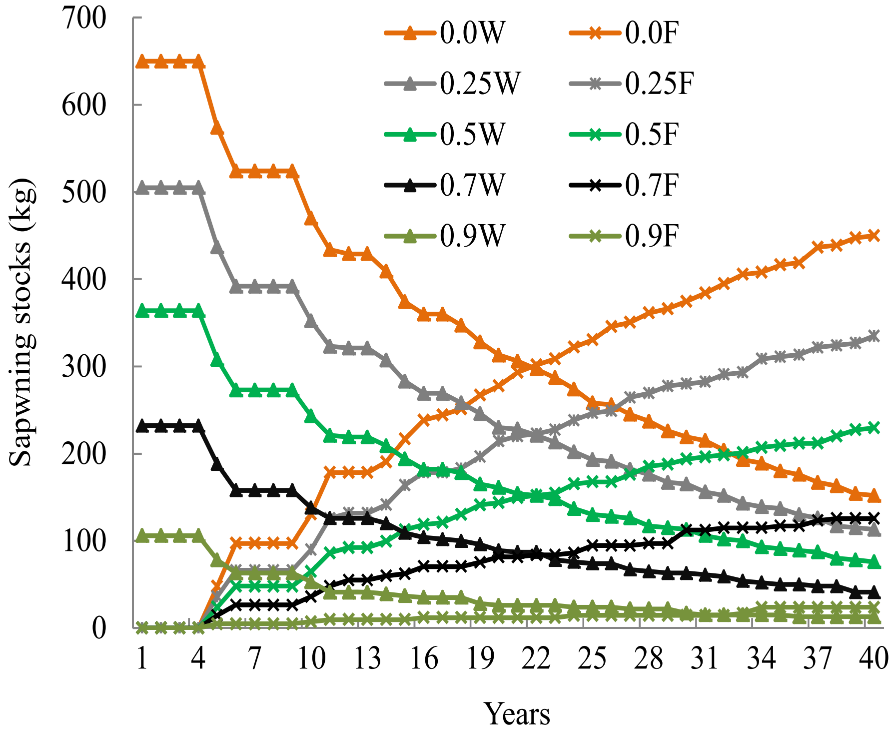

(a)
Spawning stocks in weight (kg)
0
100
200
300
400
500
600
700
1 4 7 10 13 16 19 22 25 28 31 34 37 40
Years
Unfished
0.25
0.4
0.5
0.6
0.7
0.8
0.9
(b)
Total harvest in weight (kg)
0
100
200
300
400
500
600
1 4 7 10 13 16 19 22 25 28 31 34 37 40
Years
0.9
0.8
0.7
0.6
0.5
0.4
0.25

Figure 2.



700
600
500
400
300
200
100
0
Sapwning stocks (kg)
1
4
7
10
13
16
19
22
25
28
31
34
37
40
Years
0.0W
0.0F
0.25W
0.25F
0.5W
0.5F
0.7W
0.7F
0.9W
0.9F

Figure 3.

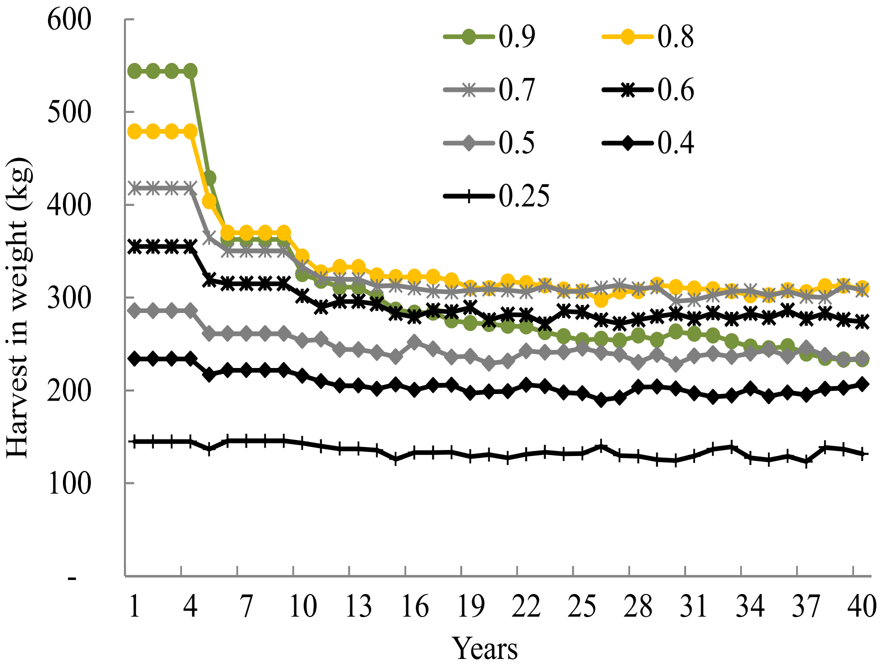
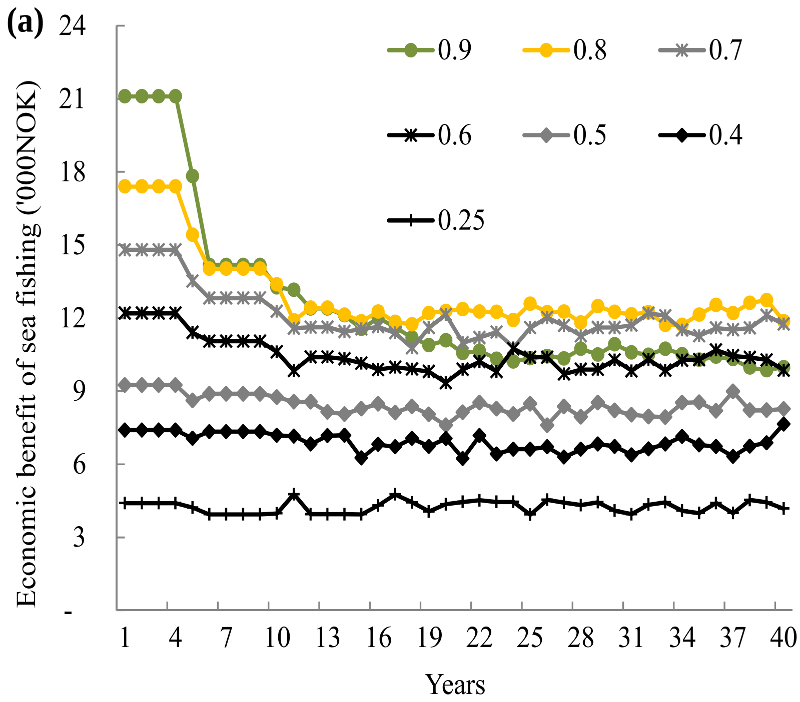
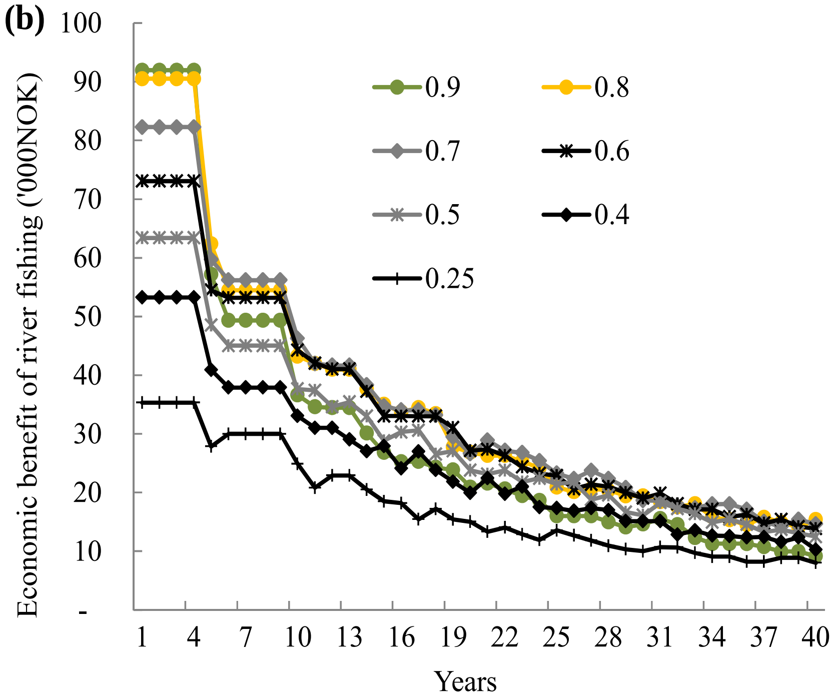

600
500
400
300
200
100
-
Harvest in weight (kg)
1 4 7 10 13 16 19 22 25 28 31 34 37 40
Years
0.9
0.8
0.7
0.6
0.5
0.4
0.25

Figure 4.



(a)
Economic benefit of sea fishing ('000NOK)
Years
0.9
0.8
0.7
0.6
0.5
0.4
0.25



(b)
Economic benefit of river fishing ('000NOK)
Years
0.9
0.8
0.7
0.6
0.5
0.4
0.25

Figure 5.

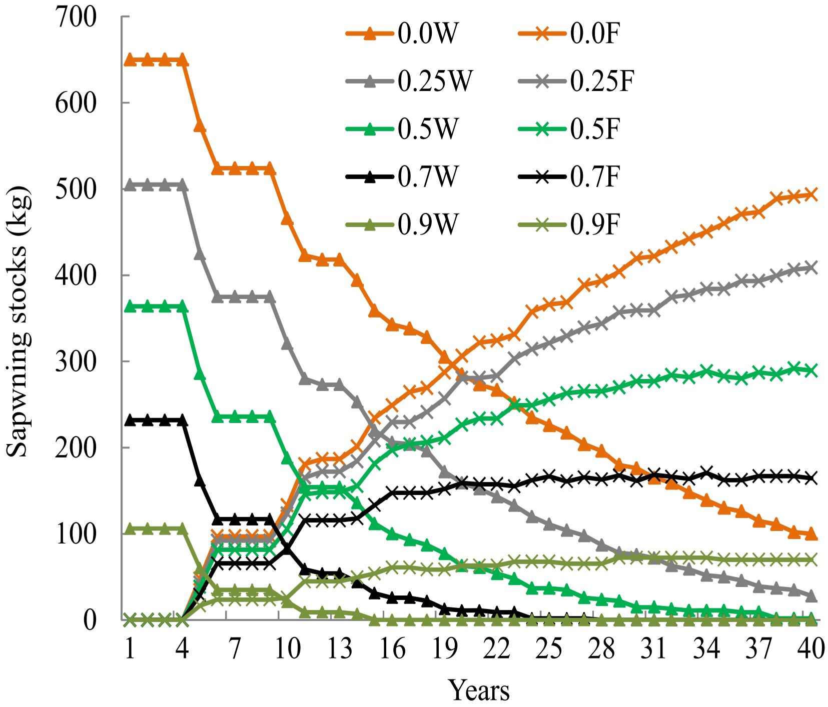

0.0W
0.0F
0.25W
0.25F
0.5W
0.5F
0.7W
0.7F
0.9W
0.9F
Sapwning stocks (kg)
Years
0
100
200
300
400
500
600
700
1
4
7
10
13
16
19
22
25
28
31
34
37
40

Figure 6.

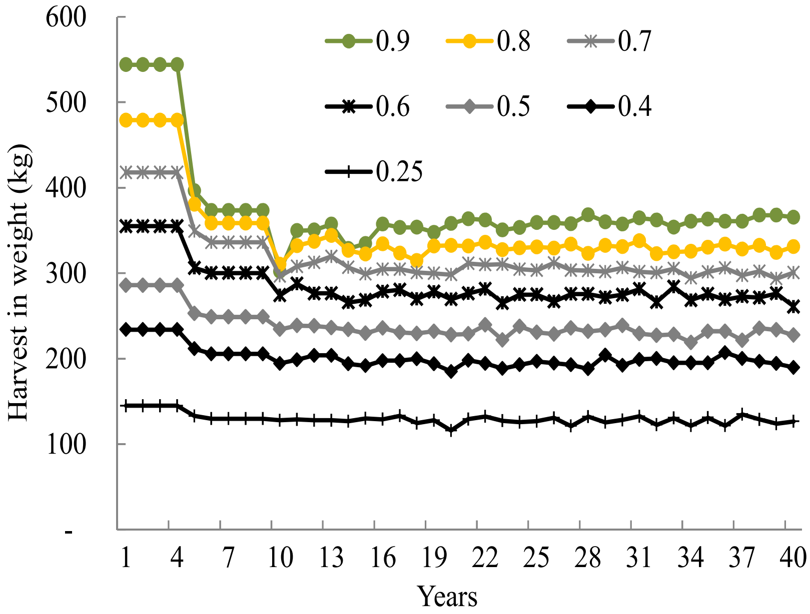
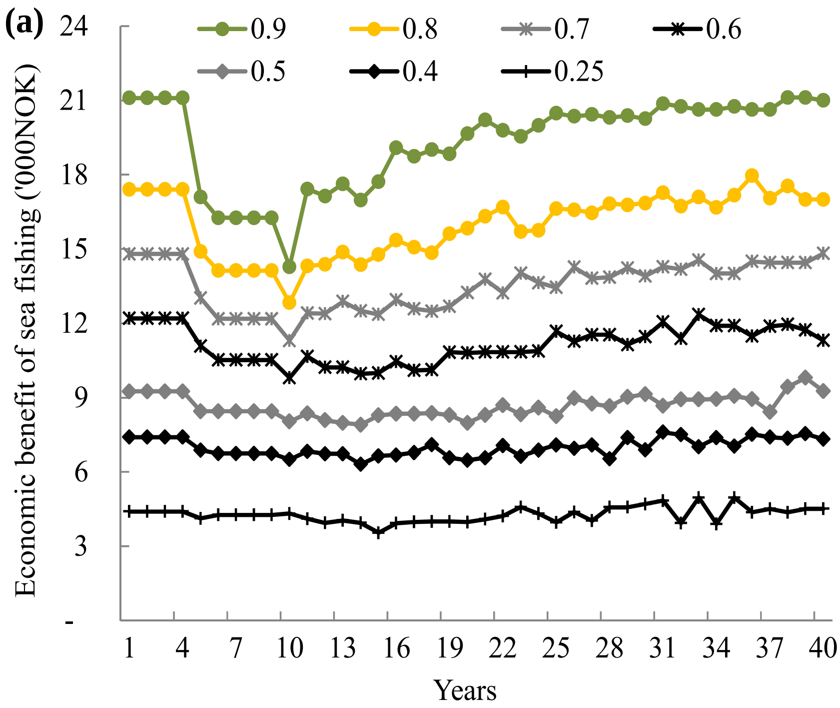

0.9
0.8
0.7
0.6
0.5
0.4
0.25
Harvest in weight (kg)
600
500
400
300
200
100
-
1
4
7
10
13
16
19
22
25
28
31
34
37
40
Years

Figure 7.


(a)
Economic benefit of sea fishing ('000NOK)
24
21
18
15
12
9
6
3
-
0.9
0.8
0.7
0.6
0.5
0.4
0.25
1
4
7
10
13
16
19
22
25
28
31
34
37
40
Years

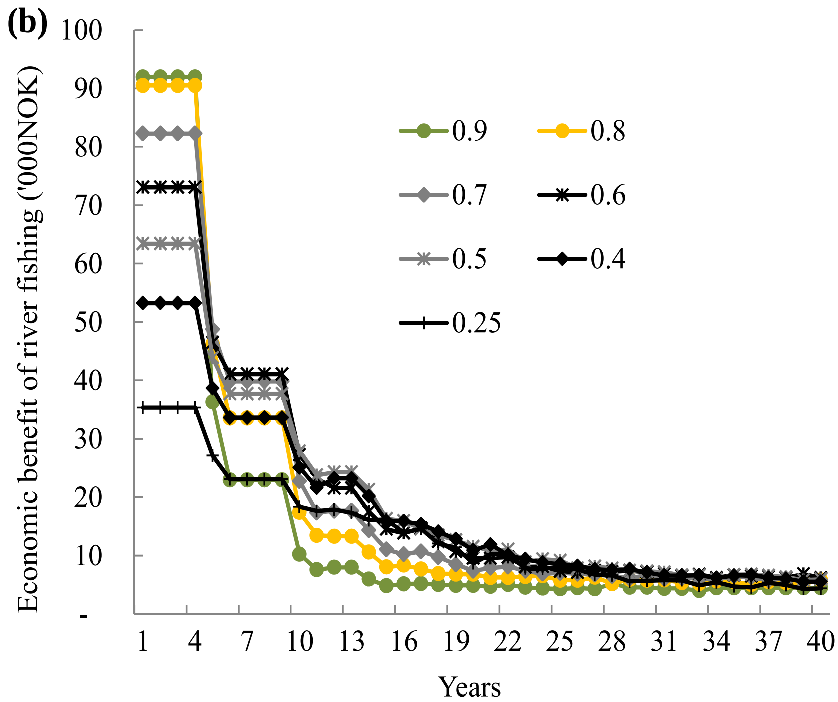

(b)
Economic benefit of river fishing ('000NOK)
100
90
80
70
60
50
40
30
20
10
-
0.9
0.8
0.7
0.6
0.5
0.4
0.25
1
4
7
10
13
16
19
22
25
28
31
34
37
40
Years

Figure 8.