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ON THE ECONOMICS OF BIOLOGICAL INVASION: AN APPLICATION TO RECREATIONAL FISHING

Jon Olaf Olaussen

Department of Economics

Norwegian University of Science and Technology
N-7491 Trondheim, Norway
www.svt.ntnu.no/iso/wp/wp.htm

On the Economics of Biological Invasion:

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Jon Olaf Olaussen

Department of Economics,

Norwegian University of Science and Technology

7491 Trondheim, Norway

e-mail: jonola@svt.ntnu.no

ABSTRACT: The paper demonstrates four general mechanisms that may affect economically valuable species when exposed to biological invasion. We distinguish between an *ecological level effect* and an *ecological growth effect*. In addition we present an *economic quantity effect* working through demand. Finally we suggest that there is an *economic quality effect* that reflects the possibility that invasions affect the harvesting agents directly through new demand-side forces. For example, this may occur because the state of the original species or the ecosystem is altered. We depart from the existing literature by revealing ecological and economic forces that explain why different agents may lack incentives to control invasions. The theoretical model is illustrated by the case where escaped farmed salmon influence wild Atlantic salmon fisheries.

Keywords: Biological invasion, escaped farmed Salmon, recreational fishing, bioeconomic model.

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1. Introduction

During the last few decades, there has been increasing concern about invasive species in various ecosystems. Holmes (1998) argued that invasive alien species are the second most important cause of biodiversity loss worldwide, beaten only by habitat alteration. In some instances, invasive species are introduced to a new environment in order to obtain some recreational or commercial gain. Perhaps the most famous case is the release of 24 wild rabbits by Thomas Austin for sport hunting on his property in Australia in 1859, which had far-reaching consequences (All-science-fair-projects 2004). In other instances, human activity indirectly has allowed intruders to establish themselves in a new environment by disturbing the natural balance in the environment, e.g. via pollution. In addition, humans have accidentally brought invasive species to new places as stowaways in cargos. One well-known example is the Zebra mussels from the Caspian Sea that were introduced to the Great Lakes in the USA via ballast water from a transoceanic vessel in the 1980s (Great Lakes Science Centre 2000). Although the economic consequences of non-indigenous species are recognized as important, there have been few attempts to quantify them. This is due to a lack of good data, as well as uncertainties and measurement problems when facing the many components that are difficult to quantify accurately (Perrings et al. 2000). One exception is Pimentel et al. (1999), who estimated total economic damages and associated control costs due to invasive species in the USA to be $138 million per year.

Several authors in Perrings et al. (2000) dealt with the economics of biological invasions. A general model set-up was given in Barbier (2001). As in Knowler and Barbier (2000), the focus was on separating the *ex-post* and *ex-ante* economic consequences of biological invasions. Knowler and Barbier studied the introduction of comb jelly (*Mnemiopsis leidyi*) in the Black Sea and its impact on the commercial Black Sea anchovy fishery. Knowler et al.

(2001) examined the extent to which pollution control could have prevented the ecological regime shift imposed by the comb jelly. Higgins et al. (1997) investigated alternative responses to the invasion of a woody species that has displaced a native plant species, in a situation where both species are valuable. Settle and Shogren (2002) developed a general model to study the introduction into Yellowstone Lake of exotic lake trout, which pose a risk to the native cutthroat trout. In their model, park managers, operating as social planners, divided their budget between controlling the lake trout and an alternative service, the improvement of a non-species good. By contrast, humans divided their time into either species consumption or spending leisure time on a non-species composite good. Eiswerth and van Kooten (2002), Horan et al. (2000), Olson and Roy (2002), and Shogren (2000) studied uncertainty with respect to species invasion. Several authors, including Buhle et al. (2004) and Hill and Greathead (2000), studied cost effective control. In a joint TC-CV study, Nunes and van den Bergh (2004) explored the extent to which people value protection against exotic species.

In this paper, we analyze yet another potential concern, namely the influence escaped farmed species may have on the natural habitants. More specifically, we study the effects that escaped farmed salmon may have on wild Atlantic salmon. Norway has been the world leader in farmed salmon since this technique was pioneered in the early 1960s. Production has risen rapidly from about 600 tonnes in 1974 to about 500 000 tonnes today (Bjørndal 1990, Statistics Norway 2004). Salmon farming is one of the most important industries in rural Norway, with a yearly first-hand value (landed value) of about 10 billion Norwegian kroner (NOK) (1.3 billion EUR). However, since the very beginning of the salmon farming industry, salmon have unintentionally been allowed to escape from net pens that are damaged by storms, seals, and otters, or by daily wear and tear. The number of accidental escapes decreased in the mid-1990s because of safety investments in the sea ranches. Nevertheless, approximately 400 000 salmon still escape yearly from fish farms in Norway (Table 1), a number exceeding the average total wild spawning stock (NOU 1999).

The wild Atlantic salmon stock is traditionally harvested in two different fisheries in Norway during its spawning run. First, the marine commercial fishery catches about 40% of the spawning biomass in fishnets in the fjords and inlets. The escapement from this fishery enters the rivers and is harvested by a recreational fishery. When the fishing season in the river closes, the escapement from these sequential fisheries takes part in the reproduction process in the river in the late autumn.

Spawning escaped farmed salmon (*EFS*) may have a number of negative effects on the natural growth and economic value of wild salmon. The most important effects are the spread of diseases and the mixing of genes through interbreeding, which affect the reproduction rate as well as the intrinsic value of the wild salmon. Farmed salmon digs in the natives’ spawning gravel, get more aggressive and risk willing offspring (NOU 1999:9), and increases the sea lice density (Grimnes et al. 1996). However, escaped farmed salmon may also have positive effects. Farmed salmon can potentially increase the salmon stock available for both marine and recreational harvests, *ceteris paribus*, and thus improve the profitability of these fisheries. As reported in table 1, escaped farmed salmon constitute a substantial part of catches. This is not to say that invasion is no problem for the society as a whole, but it may reveal economic forces inducing lack of incentives for different agents to control the invasion. These mechanisms are ignored in the previous literature.

TABLE 1 ABOUT HERE

The analysis in this paper differs from the previous studies in various ways. First, the model formulation is more general as it encompasses both *ex ante* and *ex post* effects of invasions within the same model framework. Knowler and Barbier (2000) stressed the importance of comparing the *ex ante* with the *ex-post* invasion case. We distinguish between changing ecological and economic forces, which have potentially different effects depending on the initial state. This focus allows us to depart from the stylized *ex ante* versus *ex post* framework as the biological and economic consequences may change with different levels of invasion. The constant ecological structural shift proposed by Knowler and Barbier (2000) is replaced by a shift that depends on the magnitude of the invasive influx.

Second, the general problem of invasion as a result of escapement from fish farms raises some specific new problems that have not yet been considered. We address one of these problems by explicitly taking into account the potentially ambiguous effect of biological invasion through demand-side effects. In many respects, it may be impossible for the different harvesters to separate the wild and escaped species that they catch. Hence, if invasion increases the total stock, demand may increases due to what will be called the *economic quantity effect*[1]. However, it is relatively easy to discover whether there are genetic differences or variations between the wild and the reared species through genetic investigation. Hence, knowledge about the composition of the catch, as well as the composition of the breeding stock, is often available. Thus, harvesters know the likelihood of getting a farmed instead of a wild salmon. Furthermore, harvesters may be concerned about the health of the wild stock due to crossbreeding when the share of invasive salmon in the breeding stock is high. This could be related directly to the existence value of the genetically

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[1] More generally, this effect reflects all situations in which the invasive species is connected to a harvest value.

wild species or to the loss of biodiversity due to gene flow from the reared to the wild species. Another interpretation is that harvesters simply prefer to harvest "clean" or "pure" wild Atlantic salmon. This will be called the *economic quality effect*. The two economic effects both affect the economic equilibrium condition.

Next, on the ecological side there are two effects, which work in opposite directions: the *ecological growth effect*, which is negative, and the *ecological level effect*, which is positive. In the specific case of *EFS*, the former effect reflects a general decrease in the growth rate of the wild salmon due to crossbreeding, whereas the latter reflects the yearly influx of escaped salmon that add to the total salmon stock (see below).[2] Analogous to the economic effects, these ecological effects both affects the ecological equilibrium condition.

We also analyse the consequences of invasions when there is a sequential harvest of both the invasive and the wild stock. When the composition of the catch, in terms of the share of the invasive species, differs between the various harvesters, we gain an additional management tool. By altering the share of the total harvest between the different harvesters, we can change the composition of the escapement from these sequential fisheries (Appendix B).

The rest of the paper is organized as follows. Section two formulates an ecological model for the Atlantic salmon species, and section three defines the ecological equilibrium. In section four, the economics of the river fishery are examined and the economic equilibrium condition is defined. Next, in section five, the results are combined to establish the bioeconomic

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[2] Note that in the case where genetic differences between native and alien species are high, as e.g. in Knowler and Barbier (2000), crossbreeding is not an option, and hence only the ecological growth effect applies. However, in such cases, there is clearly an analogue to this *level effect* if the invasive species is exposed to harvesting.

equilibrium. In section six, the model is illustrated by utilizing ecological and economic data from the Norwegian river Orkla. Section seven concludes the paper.

2. The Ecological Model

First, we consider a wild fish stock in the absence of escaped farmed salmon. The size of the wild population in biomass (or number of fish) at the beginning of the fishing season in year t is X_t. Both a marine and a river fishery act on the salmon during the spawning run from its offshore environment to the coast, where reproduction takes place in its parent or ´home` river. The marine fishery impacts on the stock first because this harvest takes place in the fjords and inlets before the salmon reaches their spawning river (see figure 1). For a marine harvest rate $0 \leq h_t \leq 1$, the number of wild fish removed from the population is $h_t X_t$. Accordingly, the escapement to the home river is $(1-h_t)X_t = S_{1,t}$. The river fishery exploits this spawning population along the upstream migration. When the harvesting fraction there is $0 \leq y_t \leq 1$, the river escapement is $(1-y_t)(1-h_t)X_t = (1-y_t)S_{1,t} = S_{2,t}$. This spawning stock hence yields a subsequent recruitment $R\left(S_{2,t}\right)$ to the stock in year $t+\tau$, where τ is the time lag from spawning to maturation age (see e.g. Walters, 1986).[3] Throughout the analysis, it is assumed that the stock-recruitment relationship $R(.)$ is of the Sheperd type, with $R'(.) \geq 0$, $R''(.) \leq 0$ and $R(0) = 0$ (more details below) (Sheperd 1982). The fraction of the recruits that survive up to mature age $t+\tau$ is $0 < z < 1$. Further, we assume that none of the spawners survive and we write the population dynamics when there is no invasion as $X_{t+\tau} = zR\left(S_{2,t}\right)$[4].

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[3] See Clark (1976) for an analysis of the dynamics of a delay-difference recruitment model.

[4] Hvidsten et al. (2004) find that only 0.3%-3.8% of the spawners survive justifying this simplifying assumption.

The influx of escaped farmed salmon (EFS) into the ecosystem is a yearly event. We assume that all *EFS* take part in the upstream migration. As the escapement is due to unintentional releases from the fish farms, X^F , is exogenous and not subject to an equation of motion.

As already indicated, the invasive *EFS* have two important ecological effects, the *ecological growth effect* and the *ecological level effect*. First, as in Knowler and Barbier (2000), the *ecological growth effect* reflects the fact that the population dynamics of the resident species is structurally altered by the establishment of the invader species (farmed salmon) X^F . This effect hence indicates the extent to which the growth function is negatively affected by crossbreeding (gene flow), destruction of breeding nests, and competition for food due to the invasion (see Hindar et al. 1991, Lura 1990, Lura and Sægrow 1991, McGinnity et al. (2003) and Fleming et al. (2000)). In general we allow the negative *ecological growth effect* to be increasing, decreasing or constant with the number of *EFS* (see below). The *ecological level effect*, on the other hand, reflects the fact that the *EFS* add to the wild stock through a yearly influx. Knowler and Barbier (2000) analysed a situation where the invader preys upon the resident species, and hence their model have negative effect on recruitment. In our case, a kind of predatory behaviour occurs when the *EFS* dig up wild fish spawning nests, but the *EFS* also spawn themselves. We define wild fish as all salmon that originate from river spawning. Hence, by assumption, offspring is defined as wild fish, even if recruitment may contain hybrids (crossbreedings of wild and reared salmon) and the offspring of two farmed parents.[5]

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[5] In doing so, we neglect one aspect of biological invasion because the negative effect on the gene flow due to inbreeding will continue in the next generation (Fleming et al. 2000). However, this influence on the wild fish population is partly taken into account by the structural shift (growth function shifting down).

The spawning fraction of the salmon stock is harvested together with the escaped farmed salmon, X^F (again, see figure 1). However, only a proportion of the escaped fish is available to harvest because the reared salmon typically starts its spawning migration later than the wild stock (Lura and Sægrov 1993, NOU 1999). Hence, only the fraction aX^F is available in the marine fishery, where $0 \le a \le 1$. Accordingly, with the marine fishery harvesting fraction h_t, the escapement of reared fish from the marine harvest is $(1-h_t)aX^F$. The fraction not available in the marine fishery is $(1-a)X^F$. Hence, the total stock after the marine fishery season ends is $(1-ah_t)X^F = S^F_{1,t}$. Moreover, as most of the escaped farmed salmon enter the river after the fishing season finishes, only the fraction $0 \le b \le 1$ is available for sport fishing (Fiske et al. 2000). We denote the stock that is available in the river fishery as $b(1-ah_t)X^F = bS^F_{1,t}$. Hence, with the harvesting fraction y_t, the fraction $y_t bS^F_t$ is harvested in the river. Accordingly, $(1-y_t)bS^F_t$ survives to be part of the spawning stock. In addition, the spawning stock includes the part of the stock that enters the river after the fishing season closes, $(1-b)S^F_t$. The part of the stock that enters the spawning stock in the river in a given year t is therefore $(1-by_t)S^F_{1,t} = S^F_{2,t}$. Consequently, the recruitment function with *EFS* is written as:

(1) $X_{t+\tau} = zR\left[S_{2,t} + S^F_{2,t},\ S^F_{2,t}\right]$.

The first term in the brackets represents the positive *ecological level effect* of the yearly influx of *EFS*, contributing to recruitment in the same manner as the wild stock. The negative *ecological growth effect* in the recruitment function is indicated by the last term in the brackets. Notice that this differs from Knowler and Barbier (2000), who considered a constant structural shift, whereas we consider a marginal effect from the *EFS*. Generally, the negative *ecological growth effect* may be increasing, decreasing or constant with the level of *EFS* as discussed below.

FIGURE 1 ABOUT HERE

3. The Ecological Equilibrium

In the remainder of the paper, we focus on an equilibrium model, rather than the dynamic forces, because our main goal is to establish the driving forces that follow an invasion.[6] Although we do not claim that the dynamic forces are negligible, we argue that the gain in analytical tractability from neglecting the dynamic forces offsets the loss of details in regard to the short-term dynamics.[7]

Following the approach taken by Anderson (1983, 1993), McConnel and Sutinen (1989), and Lee (1996), we measure recreational fishing effort in terms of the number of daily fishing permits sold.[8] In real life, fishing permits may be for one day, one week, or a whole season. However, as in Skonhoft and Logstein (2003), we collapse these possibilities into one-day permits because these are the most common type. Thus, the fishing effort is directly expressed in terms of the number of day permits, D. (Again, the effect of X^F is ambiguous, as will be discussed below.) We assume the offtake in the river follows the Schaefer-type harvest function. Hence, the total river yield is written as:

(2) $Y = qD\left[S_1 + bS_1^F\right]$,

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[6] For the same reason, the marine harvest rate *h* is kept in the background, entering the model exogenously.
[7] See e.g. Olaussen and Skonhoft (2005) for a dynamic analysis of recreational fishing.
[8] Others have used a different approach – for instance, Bishop and Samples (1980), Cook and McGaw (1996) and Laukkanen (2001) use the actual catch.

where Y is the total offtake, q is the catchability coefficient, and D is effort measured in number of fishing days. The content in the bracket on the right-hand side of equation (2) is the total biomass that is available in the recreational fishery. Moreover we have that the total offtake in the river per definition writes

$$(3)\quad Y = y\left[S_1 + bS_1^F\right].$$

Hence, from equation (2) and (3) it follows that the fishing mortality fraction $y = qD$. For a given marine harvest rate h, the equilibrium version of equation (1) is written

$$(4)\quad \begin{aligned} X &= zR\left(S_2 + S_2^F, S_2^F\right) = zR\left((1-qD)S_1 + (1-bqD)S_1^F, (1-bqD)S_1^F\right) \\ &= zR\left((1-qD)(1-h)X + (1-bqD)(1-ah)X^F, (1-bqD)(1-ah)X^F\right) \end{aligned}.$$

The total differential of the equilibrium condition (4) with respect to the stock and fishing effort yields $\frac{dX}{dD} = \frac{zR'\left(..\right)(S_2 + S_2^F)'_D + zR'\left(..\right)S^{F'}{}_D}{1 - zR'\left(..\right)(S_2 + S_2^F)'_X}$. Both terms in the numerator are negative as increasing the effort decreases the stock as long as $R'\left(..\right) > 0$. The denominator is positive as long as $zR'\left(..\right)(S_2 + S_2^F)'_X < 1$. Hence, we find that the ecological equilibrium condition is decreasing in the X-D plane as long as $0 < zR'\left(..\right)(S_2 + S_2^F)'_X < 1$ hold. Note that a high total spawning stock yields a low growth rate and vice versa which indicate that the condition to some extent are self-fulfilling. See also the numerical section below[9] and Appendix C for more details.

As discussed above, shifts in X^F yield two separate ecological effects, the *ecological growth effect* and the *ecological level effect*. Based on our assumptions, the growth function shifts down whenever *EFS* are present, and the marginal effect of *EFS* is constant. This means that the ecological equilibrium condition becomes steeper in the *X-D* plane due to the reduced growth rate of the species (see *Figure 2*). As we have a yearly influx of *EFS*, the *ecological level effect* operates in the opposite direction because, *ceteris paribus,* more *EFS* increase spawning. The intuition behind the *ecological level effect* is clear, because a given fishing effort is compatible with more fish when there is a yearly influx added to the stock.

FIGURE 2 ABOUT HERE

Hence, based on the two conflicting ecological mechanisms, the total stock effect depends on the initial stock size, as indicated by the shift from curve 1 to curve 1` in *Figure 2*. The *ecological level effect* of the direct invasion shifts the ecological equilibrium condition out in the *X-D* plane. At the same time, the slope becomes steeper because of the structural change (reduced growth). Increasing the marine harvest rate always makes the ecological equilibrium condition steeper. Accordingly, less fishing effort in the river is compatible with the same stock size when the marine harvest increases. The same conclusion holds for the catchability parameter, in the sense that when each angler is more effective, for example because of more effective fishing equipment, then less fishing effort in the river is compatible with the same stock size.

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[9] In the rest of the paper, we only focus on the case where $R'(..) > 0$ holds because stock sizes where $R' < 0$ are unlikely to occur in real life for Atlantic salmon (see e.g. Hansen et al. 1996 and Hvidsten et al. 2004).

4. The Economic Equilibrium

We now turn to the economic part of the model. Starting with demand, this is a question about what recreational anglers look for in the fishing experience. The price of the fishing license and the number of fishing days are expected to be important. However, as Anderson (1983), among others, emphasized, the average size of the fish caught, the total amount of fishing effort by all individuals, the anglers' income, the market price of fish, companions, and the nature of the surroundings may also play a role. However, empirical evidence shows that two of the most important determinants of fishing trip satisfaction in the Norwegian Atlantic salmon fishery are the price of permits and the size of the catch, measured as average catch per day (Fiske and Aas 2001).[10] As we focus on the issue of invasive species, we have added the above mentioned economic effects (quantity and quality) in the demand function.

The inverse demand function is hence a function of the number of fishing permits, in addition to the size of the wild and the *EFS* stock:

$$(5)\quad P = P(\overset{-}{D}, \overset{+}{X}, \overset{+/-}{X^F})\ .$$

The signs above the arguments indicate the sign of the partial derivative with respect to the number of fishing permits, D, and the signs of the shift in the inverse demand function when the wild stock and the number of *EFS* change, respectively. The inverse demand schedule is downward sloping in the number of fishing days as the willingness to pay for the fishing experience *ceteris paribus* decreases. On the other hand, it shifts upwards in the *P-D* plane

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[10] In a survey of Norwegian rivers, 92% of sport fishermen reported that the quality of the river in terms of average catch per day was important. In addition, 72% reported that the price of fishing permits was important (Fiske and Aas 2001)

when the wild stock, X , increases due to the *economic quality effect*. For a higher stock (quantity), the average catch per day increases.[11] Finally, we have the ambiguous demand effect of *EFS*. The positive *economic quantity effect* is counterbalanced by the negative *economic quality effect*. The *economic quantity effect* means that, *ceteris paribus*, the angler always regards catching one more fish as positive, even if the fish is an *EFS*. This assumption is realistic because sport fishermen are rarely able to identify a salmon as an *EFS*, especially if it is not recently escaped (NOU 1999)[12].

The *economic quality effect* is always negative as it captures fishermen's concerns about the share of *EFS* in the spawning stock.[13] One of the required attributes of a fishing experience may be that the fish are wild. When the reported share of *EFS* in the breeding stock is high, the likelihood of any catch being a farmed salmon is higher. Given that the anglers prefer the genetically "clean" wild fish, a greater *EFS*-share may reduce their willingness to pay for the fishing experience. This effect may originate from a concern about the state of a specific river's salmon stock, or simply from the fishermen's self-interested regard to their own catch, or both. However, the cause is of minor importance here, as the main point is to establish that the *economic quality effect* is negative. For a given *EFS* level, this negative effect decreases as the wild stock increases because the share of *EFS* in the total stock decreases (again, see the specification below). Moreover, the *economic quality effect* is assumed to be stronger when the share of *EFS* in the spawning stock is higher.

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[11] See also Olaussen and Skonhoft (2005) for more details on this shift in demand.

[12] Recently escaped (adult) farmed fish is often characterized by poorly developed and damaged fins, especially the caudal (tail) fin, small gills, skin bruises and general deformations. However, these signs are rarely observed when the fish escapes at an early life stage.

[13] These numbers are reported from yearly biological investigations of the spawning stock. This means that information about the average share of *EFS* in the spawning population is available and, in many cases, part of the common knowledge of anglers.

On the supply side, the landowners take into account the cost of selling fishing permits, $C(D)$. This cost is generally related to the activities undertaken by the landowners in order to provide the permit, such as advertising, administration, and supervision, as well as the construction and maintenance of parking lots, tracks, fishing huts, and so forth. Generally, there are fixed as well as variable costs.

We assume myopic, monopolistic management of the river. The traditional view is that even a very small spawning stock is able to fully replenish the river, so there is little reason for the landowners to consider the next generation stock. Therefore, they act as *de facto* myopic resource managers (treating the salmon stock as exogenous). Another possible explanation for this short-sighted behaviour is that, due to the time lag in recruitment, the landowners know that recruitment does not return for at least five years (τ=5). As the landowners cannot control the marine fishery, the harvest in the fjords induces an extra source of uncertainty about future stock. Furthermore, the argument for myopic resource management seems to be even stronger in the case of *EFS*, as *EFS* add to the complexity observed by the river manager with respect to the salmon stock. The monopolistic assumption means that the river landowners, who offer fishing permits to the recreational anglers, are able to take advantage of the downward slope of the demand curve. The assumption of monopolistic behaviour fits with the behaviour of Norwegian landowners in a typical large salmon river, where salmon tourism forms a noteworthy part of the landowner's income. By contrast, price-taking behaviour exists in many small rivers, as indicated by Olaussen and Skonhoft (2005). The river fishery profit writes $\pi = P(D, X, X^F)D - C(D)$, and accordingly, the first-order condition is:

(6) $P'_D D + P - C' = 0$.

The first-order condition gives the number of fishing permits as a function of the fish stock. Note that the stock size affects this first order-condition only through demand because the myopic landowners do not take the stock size effect into account in the profit function as mentioned above. Differentiation of the first-order condition yields $\left[2P'_D + P''_D D - C''\right] dD = -P'_X dX$. Assuming that the second-order condition for the maximum holds, the content in the bracket on the left-hand side is negative. Hence, the economic equilibrium condition is positively sloped in the *X-D* plane. The interpretation is clear-cut as more fish are compatible with more fishing permits because demand increases. The permit sale is positive only if the willingness to pay for fishing permits exceeds the cost of providing them. Hence, the minimum level of the stock must yield $P(0, X, X^F) \geq C(0)$ to ensure positive supply.

X^F influences the economic equilibrium through the *economic quantity effect* and the *economic quality effect*. Depending on which effect is dominant, the economic equilibrium condition shifts outwards or inwards in the *X-D* plane when the amount of *EFS* increases (see *Figure 2*). The *economic quantity effect* shifts the equilibrium condition inwards. This means that the fishing effort compatible with a given stock size increases because the yearly influx creates increasing demand. In addition, it indicates that the minimum stock level compatible with positive demand decreases.

On the other hand, the *economic quality effect* always shifts the equilibrium condition out because this negative effect reduces demand for a given wild stock. Which effect that dominates is an empirical question and is likely to vary from case to case, and, perhaps more important, it will depend on the initial invasion level. However, some general points can be made. One realistic assumption seems to be that the *economic quality effect* will diminish with an increasing wild stock. In other words, the higher is the proportion of wild salmon in the total stock, the smaller will be the share of the *EFS* in the spawning population. Accordingly, the negative *economic quality effect* will be less. The basic idea is that the initial situation affects how a change in the number of *EFS* operates. In the *P-D* plane, this means that for a given initial stock, increasing levels of X^F shifts the inverse demand schedule up if the *economic quantity effect* dominates the *economic quality effect* and the vice versa. Moreover, for a given effort level, the inverse demand schedule is more concave in the *P-X* plane when $X^F > 0$ (see also numerical section below). This assumptions leads to the economic equilibrium condition depicted in *Figure 2*, where the *economic quality effect* dominates the *economic quantity effect* only for small initial wild stock sizes. The same line of arguing indicates that if the *economic quality effect* is low, then there is a greater likelihood that *D* will increase as the number of *EFS* increases. Moreover, if there is no *economic quality effect*, the curve simply shifts unambiguously inwards in the *X-D* plane due to the positive *economic quantity effect*. In addition, notice that the *economic quality effect* means that if the wild stock changes, demand respond more in the post- than in the pre-invasion case. This is because, post-invasion, there is an additional demand effect induced by the changing composition of the spawning stock.

5. The Bioeconomic Equilibrium

As illustrated in *Figure 2*, the bioeconomic equilibrium, in which both the ecological and economic equilibrium conditions are satisfied, is represented by the interception between the curves. Comparing the pre- and post-invasion states, that is, comparing $X^F = 0$ (curves 1 and 2) with X^F>0 (curves 1` and 2`), we find that the effects on stock (X) and effort (D) are both ambiguous. This follows directly since both equilibrium conditions shift simultaneously. The fact that the bioeconomic result of an invasion directly depends on the initial state highlights the importance of separating between different initial levels of invasion.

If we concentrate on the difference between the pre-and the post-invasion situations, we are required to take all four effects into account. Moreover, if we are already in a post-invasion environment, all effects will still apply. As discussed above, and shown in *Figure 2*, it is not possible to make general statements about the stock and the number of fishing days when we have changes in the number of *EFS*. As noted, the initial situation is an important determinant of the consequences for stock and effort flowing from an increased invasion. For a given level of invasion, we find that when the level of the wild stock is low, the share of reared salmon in the spawning stock is relatively high. This means that the *economic quality effect* will be important, placing us on the steeper part of the economic equilibrium condition depicted in *Figure 2*. From this equilibrium, we know that the schedule shifts down and rises more steeply in the *X-D* plane at the same time. From the ecological equilibrium schedule, we find that the slope is flatter when the stock is low (the convex ecological equilibrium schedule), increasing the likelihood that X will increase as the number of *EFS* increases (see *Figure* 2). Thus, both the ecological and the economic forces operate in the same direction when the initial stock level is low.

If we turn to a situation where the level of the wild stock is high, then the share of invasive fish in the spawning stock is small, making the *economic quality effect* negligible to the sport anglers. As noted above, *ceteris paribus* this increases the likelihood that fishing effort will increase with an increase in the number of *EFS*. However, due to the steep fall in the ecological condition when the stock is high, the bioeconomic result is more likely to reduce stock and effort, as indicated in *Figure 3*. To come to more definite conclusions about the magnitude of the different effects, we illustrate the model with an example based on the Norwegian Salmon River Orkla.

FIGURE 3 ABOUT HERE

6. A Numerical Illustration

6.1 Data and specific functional forms

The biological data are in accordance with a typical large Atlantic salmon river in Norway, as represented by the river Orkla, which is situated some 500 km north of Oslo. A biological investigation conducted by Hvidsten et al. (2004) provides the only data available worldwide that estimates the recruitment function in a large Atlantic salmon river. Moreover, the Orkla River is one of the "cleanest" large salmon rivers in Norway with respect to biological invasion. It has low levels of escaped farmed salmon in both catch statistics and the spawning population – according to Fiske et al. (2000), these levels average 1% and 18%, respectively. In the marine fisheries, Fiske et al. (2000) showed that, on average, 32% of the marine offtake is made up of *EFS* (see Appendix A for a calibration of the biological model). Biological research suggest that the recruitment function $R(..)$ is close to the Beverton Holt type, but that neither the Cushing nor the Ricker type recruitement can be ruled out. It is therefore convenient to write it as the Sheperd (1982) recruitment function[14]:

$$(7)\ \ R(..) = \left[\frac{r(1-\varepsilon\left(S_2^F\right)^{\eta})\left[S_2 + S_2^F\right]}{1+\left(\frac{\left[S_2 + S_2^F\right]}{K}\right)^{\gamma}} \right],$$

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[14] The Sheperd function produces the Cushing recruitment function when $\gamma<1$, the Beverton Holt recruitment function when $\gamma=1$, and the Ricker recruitment function when $\gamma>1$.

where *r* is the maximum recruits per spawning salmon, and *K* is the stock level where density dependent mortality factors start to dominate stock independent factors.[15] Finally, the compensation parameter γ is the degree to which density-independent effects compensate for changes in stock size. The baseline parameter values are given in Appendix A**.** The pre-invasion recruitment is found by setting $X^F = 0$. Note that the marginal negative *ecological growth effect* of *EFS* is constant when $\eta = 1$, decreasing for $\eta < 1$, and increasing when $\eta > 1$. In the numerical simulations we assume $\eta = 1$ and that the restriction $\varepsilon\left(X^F\right) < 1$ holds[16].

Turning to the economic functions, we start out by defining the inverse demand function when there are no *EFS* (pre invasion):

(8) $P(D, X, X^F) = \alpha q S_1 - \beta D$.

The choke price α gives the maximum willingness to pay when the quality-translated catch is one fish per day, whereas β reflects the price response in a standard manner. In the case of invasion, the inverse demand function is specified as follows

(9) $P(D, X, X^F) = \alpha q\left[S_1 + bS_1^F\right] - \beta D - w\left(\frac{\left(S_2^F\right)^\theta}{S_2}\right)$.

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[15] Note that the numbers reported in Hvidsten et al. (2004) are measured as recruits per egg per square metre. However, we have translated them into the corresponding number of recruits per spawning salmon in the river (available on request).

[16] Fleming et al (2000) show in a controlled experiment that the productivity of the natives are depressed by 30% when the share of farmed to natives in the spawning population were 57%. However, if there is an increasing or decreasing marginal negative impact is not analysed as it is a one-shot experiment.

Note that equation (9) reduces to (8) when there are no *EFS* present. The ambiguous demand effects following *EFS* are easiliy recognised in equation (9). The demand increases via the catch per day-channel inducing the *economic quantity effect* in the term $\alpha q S_1^F$. On the other hand, the proportion of farmed fish in the total stock increases, leading to the *economic quality effect* that operates via the last term on the right-hand side. The specification of the *economic quality effect* means that when X^F>0, the inverse demand increases at a decreasing rate with X in the P-X plane, as explained in section 4. This means that the smaller the level of the wild stock is, the more the increased invasion reduces demand through the *economic quality effect* (more on this below). All parameters are defined and the baseline values are given in Appendix A. Finally, the cost function is specified as $C(D) = c_0 + cD$, where c_0 and c are the fixed and the marginal costs of providing fishing permits, respectively. With these specifications, in the post-invasion case, we express the number of fishing permits from the first-order condition, $\frac{d\pi}{dD} = 0$, as:

$$(10)\quad D = \frac{\left[\alpha q \left(S_1 + S_1^F \right) - c - w \frac{\left[S_2^F \right]^{\theta}}{S_2} \right]}{2\beta}.$$

The pre-invasion demand is found simply by introducing $X^F = 0$ (and thus $S_1^F = S_2^F = 0$). Note that although the share of *EFS* in the spawning stock influences demand directly, equation (10) reflects the fact that landowners do not see their own fishing permit sales as an instrument to influence this share. One possible reason for this is that a very small proportion of the river catch consists of *EFS*. On the other hand, this would be an argument for the landowners to decrease their harvest in order to increase the share of wild salmon in the spawning stock. However, consistent with our assumption that they are myopic, the landowners ignore the spawning stock, including the composition of wild and farmed spawners. Note that with no *economic quality effect* in demand, $w = 0$, the equilibrium condition shifts up in the *X-D* plane when $X^F > 0$, and that the slope of the equilibrium condition changes when $w > 0$ and $X^F > 0$ (see also discussion above and Appendix C for details). Recall also that *D* is more likely to increase in X^F, the higher X is, as the negative *economic quality effect* diminishes. In addition, we find that when demand is generally higher for a given stock size, as indicated by an increase in α, then D is more likely to increase with X^F. By contrast and for obvious reasons, when anglers are more concerned about negative *EFS* effects ($w \uparrow$) this works in the other direction.

6.2 Results

Table 2 reports the results in the pre- and post-invasion situations with the baseline parameter values. Note that the escapement only modestly affects the stock because the *EFS* have two contradictory effects on the wild stock (see above). Consequently, in the post-invasion case, the marginal stock change is largest when the escapement rate is low. For example, this could be a situation where safety investments in the sea farming industry have reduced the escapement rate, or where aquaculture is abandoned in some fjords in order to establish national farming free zones.[17] In addition, notice that the fishing effort increases when the number of *EFS* shifts from the pre-invasion case, where EFS=0, to the post-invasion case, where *EFS*=2000, and it is almost the same as pre-invasion when *EFS*=4000. However, increasing the number of *EFS* further decreases the fishing effort because of the increasing *economic quality effect,* even if the stock increases. In addition, notice that the wild stock is not strictly increasing with an increased level of *EFS*, meaning that, for the baseline parameter

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[17] The Norwegian government imposed this regulation on some fjords in 2003. The fjord where the river Orkla runs out (Trondheimsfjorden) was established as one of the farming free zones.

values, the negative *ecological growth effect* dominates when the proportion of *EFS* reaches a certain level.

TABLE 2 ABOUT HERE

Further, in the post-invasion situation, we find that the profit may rise because of an increase in the invasive stock (the direct *economic quantity effect*). Comparing *EFS*=0 and *EFS*=2 shows that the stock increase causes an increase in the number of fishing days, without affecting the permit price. This highlights an important fact, which is that, given an invasion, the equilibrium profit may rise with an increasing yearly influx. In other words, the yearly influx may hide the reduced biomass production rate. However, as long as the share of *EFS* in the spawning stock matters to the anglers, then a higher invasion level will mean the *economic quality effect* increases in importance. Hence, the fishing effort and profits may fall dramatically. Note that the angler surplus, and thus the total surplus in the river, follows the exact same pattern as the monopolistic profit. The decreasing price follows directly from the negative *economic quality effect* on demand. For the baseline invasion level, *EFS*=6000, the *EFS* levels in the marine harvest and the river harvest are 25% and 8% respectively, whereas 48% of the spawning stock consists of *EFS*.

Now, we turn to a situation where the anglers consider "a fish as a fish", both in their harvest and in the spawning stock.[18] This means that the last term in the inverse demand function is neglected, *w*=0. The only way that the *EFS* translate directly into demand is through the effect on the overall stock. The stock increases modestly as the number of *EFS* increases. In addition, both the fishing effort and permit prices increase due to the *economic quantity effect.*

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[18] i.e. anglers are not concerned whether salmon is farmed or wild

The results reported in table 3 hence reflect this situation, where the *ecological level effect* on the wild stock dominates the *ecological growth effect*. Thus, one problematic aspect of invasion is hidden when there is no *economic quality effect*. When the *economic quality effect* applies, the *ex-post* wild stock is always higher than in the absence of this effect. This is because the fishing effort is higher when anglers are not concerned about the number of reared fish in the population.

The profit, the angler surplus, and hence, the total surplus, are strictly increasing as the number of *EFS* increases. In the baseline case when *EFS*=6000, 26% of the marine harvest, 9% of the river sport harvest, and 71% of the spawning stock consist of farmed salmon. This means that when there is an *economic quality effect*, the proportion of farmed to wild salmon in the spawning stock is reduced. However, the manner in which the concern about invasive species reduces this share through the *economic quality effect* is not straightforward. When demand is reduced because of the *economic quality effect*, the share of wild salmon in the spawning stock increases relative to the reared salmon share because the anglers mainly catch wild fish. Therefore, the mechanism is not the result of any deliberate action by the anglers to decrease the share of reared fish in the spawning stock, but rather, it is a fortunate consequence of reduced demand.

TABLE 3 ABOUT HERE

7. Concluding Remarks

The paper demonstrates four different mechanisms that may be important when escaped reared species mix with their wild congeners, and thereby, we reveal some important policy implications. Our results indicate that, even if the growth rate of the wild species is reduced, the total stock may increase when there is an ecological invasion. Hence, measures to reduce an invasion may very well reduce the overall surplus because less biomass will be available for harvest. On interesting result is that, if there is no *economic quality effect,* the harvesting effort will be higher due to the *economic quantity effect* and, hence, the stock will be less than before the invasion. In this case, the profit and the angler surplus will always be higher *ex post* the invasion, and both will increase with invasion of the farmed species. Thus, one consequence that follows directly from the analyses is that reporting the share of invasive species in an ecosystem may reduce the demand for harvesting the wild species. This will in turn increase the wild stock and depending on the composition of the catch, the share of resident species in the ecosystem may increase. Finally, the effect on overall surplus of shutting down one sequential harvest activity in the case of an invasion is generally ambiguous because the share of the invasive species in the spawning population (or ecosystem) may increase (see Appendix B).

The mechanisms discussed in the paper may be transferable to other situations where escaped farmed animals mix with their wild congeners, or where an ecosystem faces a yearly influx of invasive species for any reason. We have demonstrated that, even taking invasive damage into account, in many instances, the overall surplus may rise following an invasion. Of course, this may have implications for incentives to reduce the escapement of farmed species. As shown, participants in the harvest may want invasions to persist. Perhaps more importantly, these economic forces, or lack of incentives, may explain why policymakers must intervene if they want to reduce invasions. On the other hand, one interesting extension of the model developed here is to incorporate a social planner managing both the marine and the recreational fishery, as the outcome of such planning with respect to profit, angler surplus and share of invasive in the spawning stock seems far from clear cut. Making the model more realistic by including the spread of diseases and stochastic elements, and by taking existence value more explicitly into account, may alter some of the results. Nevertheless, the general driving forces described in the paper offer some general insights into the bioeconomics of ecological invasions.

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Appendix A

Data and calibration

Table A1: Baseline values prices and costs, ecological and other parameters

Parameter	Parameter description	Value
r	Maximum recruitment per spawning salmon	270 (smolt per spawning salmon)
γ	Decides to which extent density independent factors compensates for stock changes	1.06
K	Stock level where density dependent mortality dominates density independent factors	1489 (number of spawning salmon)
s	Survival rate recruits	0.05
α	Reservation price when catch per day is 1	500 (NOK/salmon)
β	Price effect demand	0.12 (NOK/day^2)
c	Marginal cost fishing permit sale	50 (NOK/day)
c_0	Fixed cost fishing permit sale	0
q	Catchability coefficient	0.0002 (1/day)
h	Marine harvest rate	0.3
y	River harvest rate	0.58
τ	Time lag recruitment spawner	5 years
X^F	Invasive yearly influx	6000
ε	Negative impact recruitment by invasive	0.00001
η	Decides if the negative marginal ecological growth effect of EFS is increasing, decreasing or constant	1
a	Share of invasive available for marine fishery	0.8
b	Share of invasive available for river fishery	0.2
w	Price effect share of invasive	0.1
θ	Decides if the negative marginal price effect of share of invasive is increasing, decreasing or constant	2

Appendix B: Closing down the marine fishery

We consider measures to change the composition of catches in the marine and river fisheries. More specifically, table 4 reports the results of a sea fishing ban. It is often argued that a sea fishing ban increases the overall profitability in salmon fisheries because the value of a sea-caught salmon is more or less directly related to the meat value, whereas a river-caught salmon exceeds the meat value by several times (see Olaussen and Skonhoft 2005). As a direct response to a sea fishing ban, more fish enter the river and river catches increase for a given total stock size due to increased fishing effort. For a given number of fishing days, the price of permits increases due to the increased catch per day. The fishing effort is consistently higher under a sea fishing ban than when the marine harvest rate is positive. However, the total quantity effect is ambiguous because more fish enter the river. In addition, the profit exceeds the baseline profits for all levels of EFS. However, when EFS=6000, only 8% of the total EFS stock is harvested, leaving the remaining 92% to take part in the spawning process. Hence, 57% of the spawning biomass is EFS.

TABLE B1 ABOUT HERE

Appendix C: Comparative statics

Ecological equilibrium:

$$X = \frac{zr(1-\varepsilon\left(X^F\right)^{\eta})K^{\gamma}\left[(1-qD)\left(1-h\right)X+(1-bqD)\left(1-ah\right)X^F\right]}{\left[K^{\gamma}+\left[(1-qD)\left(1-h\right)X+(1-bqD)\left(1-ah\right)X^F\right]^{\gamma}\right]}$$

If we define

$$V=\left[K^{\gamma}+\left[(1-qD)\left(1-h\right)X+(1-bqD)\left(1-ah\right)X^F\right]^{\gamma}\right]$$

and

$$W=\left[(1-qD)\left(1-h\right)X+(1-bqD)\left(1-ah\right)X^F\right]$$

then

$$\left(1-\left(\frac{1}{V^2}\right)\left\{\ zr(1-\varepsilon\left(X^F\right)^{\eta})K^{\gamma}(1-qD)\left(1-h\right)\cdot V-zr(1-\varepsilon\left(X^F\right)^{\eta})K^{\gamma}\gamma W^{\gamma}(1-qD)\left(1-h\right)\ \right\}\right)dX=$$

$$=\left(\frac{1}{\left[V\right]^2}\right)\left\{-zr(1-\varepsilon\left(X^F\right)^{\eta})K^{\gamma}\left(q(1-h)X+bq\left(1-ah\right)X^F\right)V+\gamma W^{\gamma-1}\left\{q\left(1-h\right)X+bq\left(1-ah\right)X^F\right\}zr(1-\varepsilon\left(X^F\right)^{\eta})K^{\gamma}W\ \right\}dD$$

Thus

$$\frac{dX}{dD}=\frac{\left\{zr(1-\varepsilon\left(X^F\right)^{\eta})K^{\gamma}\left\{q\left(1-h\right)X+bq\left(1-ah\right)X^F\right\}\right.}{V^2\left[\gamma\left[W\right]^{\gamma}-V\right]^{-1}+zr(1-\varepsilon\left(X^F\right)^{\eta})K^{\gamma}(1-qD)\left(1-h\right)}$$

which is negative as long as $V^2\left[\gamma[W]^\gamma - V\right]^{-1} + zr(1-\varepsilon X^F)K^\gamma(1-qD)\left(1-h\right) < 0$. Note that as the recruitment function approaches the Beverton Holt shape, the likelihood of a negative $\left[\gamma[W]^\gamma - V\right]$ increases. Moreover, $\gamma \leq 1$ (Beverton-Holt (*γ=1)* or Cushing (*γ<1)* recruitement function) ensures that $\left[\gamma[W]^\gamma - V\right] < 0$.

$$\frac{dX}{dX^F} = -\frac{zr\varepsilon K^\gamma\left[W\right]}{\left[V\right]} + \frac{zr(1-\varepsilon X^F)K^\gamma(1-bqD)\left(1-ah\right)}{\left[V\right]} - \frac{zr(1-\varepsilon X^F)K^\gamma\left[W^\gamma \gamma(1-bqD)\left(1-ah\right)\right]}{\left[V\right]^2} \begin{smallmatrix} > \\ < \end{smallmatrix} 0$$

Economic equilibrium:

$$\frac{dD}{dX} = \frac{\left[\alpha q(1-h) + w\dfrac{\left[\left(1-ah\right)\left(1-bqD\right)\left(X^F\right)\right]^2}{(1-h)(1-qD)X^2}\right]}{2\beta - w\left[\dfrac{2\left[\left(1-ah\right)\left(X^F\right)\right]^2 bq(1-h)(1-qD)X - q(1-h)X\left[\left(1-ah\right)\left(1-bqD\right)\left(X^F\right)\right]^2}{\left((1-h)(1-qD)X\right)^2}\right]}$$

which is clearly identical with the slope of the equilibrium condition in the case of no invasion as long as the *economic quality effect* is zero (w=0). Moreover, a sufficient but not necessary condition for the slope to be steeper in the *X-D* plane with the *economic quality effect* present is that $2b > 1-\left(bqD\right)^2$. Note also that *ceteris paribus*, when *X* increases, the slope approaches the linear case with no *economic quality effect.*

$$\frac{dD}{dX^F} = \frac{\left[\alpha q(1-ah)b - 2w\frac{\left(\left(1-ah\right)\left(1-bqD\right)\right)^2 X^F}{(1-h)(1-qD)X} \right]}{2\beta - w\left[\frac{2\left[\left(1-ah\right)\left(X^F\right)\right]^2 bq(1-h)(1-qD)X - q(1-h)X\left[\left(1-ah\right)\left(1-bqD\right)\left(X^F\right)\right]^2}{\left((1-h)(1-qD)X\right)^2} \right]} \underset{<}{\overset{>}{-}} 0$$

Tables and Figures

Table 1: Escaped farmed salmon (*EFS*) in Norwegian fisheries and river spawning stocks, 1989-2003.

Year	Total number of *EFS* (1000)	*EFS* share of total catch in river fishery(%)	*EFS* share of total catch in marine fishery (%)*	*EFS* share in spawning stock (%)
1989	-	7	30	35
1990	-	7	32	34
1991	-	5	30	24
1992	-	5	33	26
1993	498	5	34	22
1994	536	4	28	22
1995	240	5	28	29
1996	417	7	32	31
1997	506	9	40	29
1998	553	9	38	22
1999	348	6	33	15
2000	276	7	24	11
2001	272	7	23	11
2002	475	16	31	18
2003	240		18	13
Average, 1989-2002 periode	412	7%	31%	24%

Source: http://www.miljostatus.no/templates/PageWithRightListing____2236.aspx

[*] Un-weighted average, coast+ fjord.

[**] Preliminary estimates

Table 2: Pre- and post-invasion results for stock X (in 1000), number of day permits D(in 1000), price of day permits P (1000 NOK), Recreational angler (consumer) surplus AS (1000 NOK), monopoly profits π (1000 NOK), and total surplus (TS) for different levels of escaped farmed salmon, *EFS* (in 1000).

	Pre-invasion	Post-invasion				
	EFS =0	*EFS*=2	*EFS*=4	*EFS*=6	*EFS*=8	*EFS*=10
X	12.6	13.7	14.4	14.7	14.7	14.5
D	3.5	3.6	3.4	2.9	2.3	1.6
P	0.5	0.5	0.5	0.4	0.3	0.2
AS	727	794	683	501	314	152
π	1453	1588	1366	1003	628	304
TS	2180	2382	2049	1504	942	456

Table 3: No *economic quality effect*. Pre- and post-invasion results for stock X (in 1000), number of day permits D(in 1000), price of day permits P (1000 NOK), Recreational angler (consumer) surplus AS (1000 NOK), monopoly profits π (1000 NOK), and total surplus (TS) for different levels of escaped farmed salmon, *EFS* (in 1000).

	Pre-invasion	Post-invasion				
	EFS =0	*EFS*=2	*EFS*=4	*EFS*=6	*EFS*=8	*EFS*=10
X	12.6	13.3	13.7	13.9	13.9	13.9
D	3.5	3.8	4.0	4.2	4.4	4.5
P	0.5	0.5	0.5	0.6	0.6	0.6
AS	727	871	982	1070	1141	1199
π	1453	1741	1964	2141	2282	2397
TS	2180	2612	2946	3211	3423	3596

Table B1: No marine harvest. Pre- and post-invasion results for stock X (in 1000), number of day permits D(in 1000), price of day permits P (1000 NOK), Recreational angler (consumer) surplus AS (1000 NOK), monopoly profits π (1000 NOK), and total surplus (TS) for different levels of escaped farmed salmon, *EFS* (in 1000).

	Pre-invasion	Post-invasion				
	EFS =0	*EFS*=2	*EFS*=4	*EFS*=6	*EFS*=8	*EFS*=10
X	10.6	12.8	14.4	14.8	14.7	14.5
D	4.2	4.5	4.2	3.7	3.0	2.3
P	0.6	0.6	0.6	0.5	0.4	0.3
AS	1063	1198	1042	808	555	318
π	2127	2396	2085	1616	1110	635
TS	3190	3594	3127	2424	1665	953

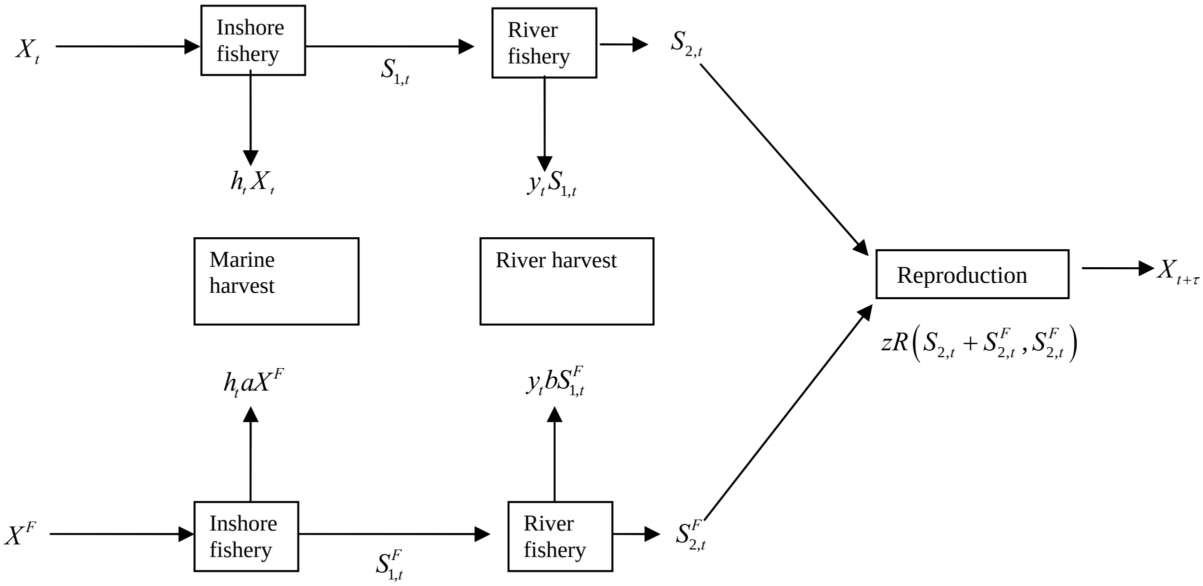

Figure 1: Harvest and reproduction
Wild salmon, X_t, Escaped farmed salmon, X^F, marine harvest rate, h_t, river harvest rate, y_t share of escaped farmed fish available for marine and river harvest, a and b, respectively, growth function, $R(..)$, share of recruits surviving from recruitment up to mature age, z, time lag from recruitment to maturation age, τ.

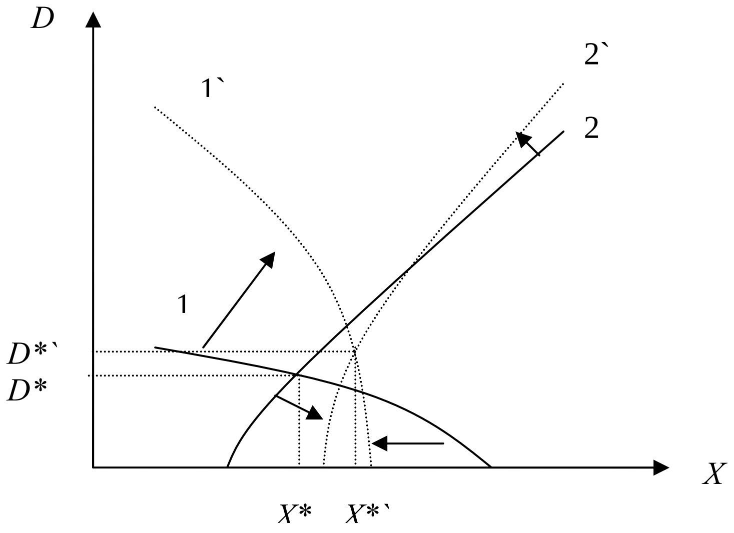

Figure 2: Bioeconomic equilibrium.
Pre-invasion (initial) state: curve 1 depicts the ecological equilibrium and graph 2 illustrates the economic equilibrium. Bioeconomic equilibrium is given by *X** and *D**.
Post-invasion state: The 1` and 2`curves describes the ecological and economic equilibrium respectively with X^F>0. Bioeconomic equilibrium is given by *X**` and *D\**`.

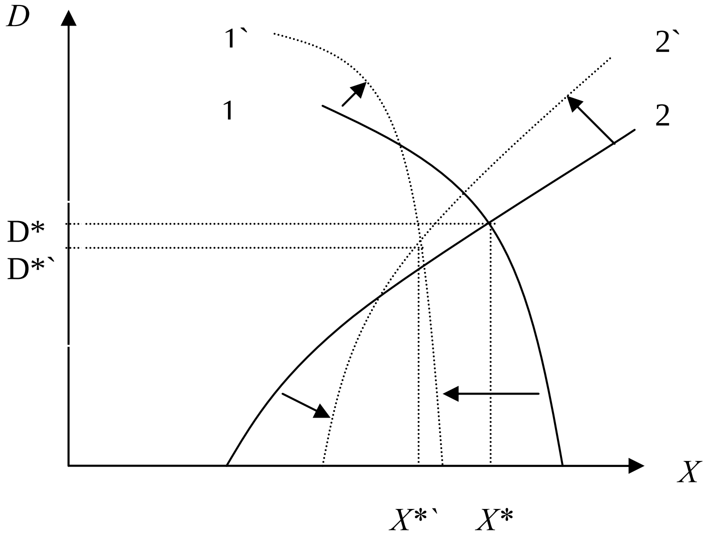

Figure 3: Bioeconomic equilibrium. High initial wild stock.
Pre-invasion (initial) state: curve 1 depicts the ecological equilibrium and graph 2 illustrates the economic equilibrium. Bioeconomic equilibrium is given by *X** and *D**.
Post-invasion state: The 1` and 2`curves describes the ecological and economic equilibrium respectively with X^F>0. Bioeconomic equilibrium is given by *X**` and *D\**`.