Conservation versus harvest of wild Atlantic salmon. The cost of sea lice induced mortality

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Abstract

Increased sea lice densities in the farmed salmon sector have recently led to the growing concerns in Canada, Chile and Norway as the main producer countries. The sea lice incur problems within the farmed fish industry itself as well as in wild stocks. We present a bioeconomic model for wild Atlantic salmon (*Salmo salar*) and explore to what extent the harvest and social benefit of wild salmon fishing in Norway are affected by sea lice-induced mortality. An age-structured population model is required to analyze the losses because the salmon post-smolts are the most vulnerable to attack by sea lice, while the harvest value is related to the three age classes of mature spawning fish. Losses are analyzed by determining the reduced harvesting value as well as the non-consumptive (conservation) value of the wild salmon stock pertinent to various sea lice-induced mortality levels. Our findings indicate that welfare and economic losses in a typical Norwegian salmon river may range from 15 to 25%. In addition, at low sea lice levels, the welfare improvement associated with selective harvest is quite modest, and is even lower when non-consumptive values are deemed important. On the other hand, when sea lice-induced mortality levels are very high, the welfare improvements of selective harvest are substantial.

Key words: Atlantic salmon, sea lice, conservation, welfare loss, age structured model, management

1. Introduction

We present an analysis of wild Atlantic salmon (*Salmo salar*) management in Norway. The great number of salmon rivers in Norway offers the world`s largest spawning ground for Atlantic salmon. Wild salmon has long had significant social, cultural and economic importance for Norwegians. Previously an important food source, today, it is mainly the prized catch for approximately 100,000 recreational anglers that visit these rivers annually. Wild salmon is also valued for its mere existence, as this is a natural treasure that has significant conservation value. Atlantic salmon stocks have declined during the last few decades. One of the most important challenges the wild stocks face is the growing aquaculture industry (NOU, 1999; Fiske et al., 2006; Ford and Myers, 2008; Liu et al., 2011a). The wild population is affected by aquaculture primarily through escaped farmed salmon and by increasing density of sea lice (*Lepeophtheirus salmonis* and *Caligus clemensi*). Both these problems emerged soon after the establishment of the farming industry in the 1970s (Heuch et al., 2005). Escaped farmed salmon interbreed and have genetic interactions with the wild populations. This phenomenon was investigated by Liu et al. (2013) and Hindar et al. (2006), who found that the wild salmon stock is gradually being replaced by salmon with farmed origin. Aquaculture production has also resulted in increased prevalence of sea lice attacks on out-migrating salmon, which is the issue addressed here. In a related study, Liu et al. (2011b) investigated the impacts of sea lice on wild pink and chum salmon fisheries.

The collective term “sea lice” normally refers to a number of copepod crustaceans of the family *Caligidae* (Revie et al., 2009). Sea lice are externally parasitic on the skin of marine and anadromous species. The most common and extensively studied species is the *Lepeophtheirus salmonis,* which is a parasite specific to salmonid species. This parasite is prevalent in both Atlantic and Pacific Ocean, and the Chilean farming industry also experiences challenges with *Caligus teres* and *Caligus rogercresseyi* (Revie et al., 2009). The lice are mainly a problem for the salmon post-smolts on their seaward migration journey, as they have to pass the fish farms before they reach their offshore winter habitat. According to the recent report from the scientific advisory board for salmon management in Norway, the high sea lice densities and escaped farmed salmon from aquaculture are the two most significant and existential threats to the wild salmon populations in Norway (Anon, 2014). Salmon aquaculture increases the sea lice density in the fjords and along the coast because they amplify the number of hosts for the lice by a factor of 100 (Heuch et al., 2005). Smolt infected by less than 10 sea lice are considered to be unaffected by the parasite. Empirical evidence, however, seems to suggest that this threshold level is too high, as only smolt with 10 lice or fewer survive (Heuch et al., 2005; Holst et al., 2003). In some cases, surveillance studies have revealed that up to 100 sea lice per smolt are not uncommon (Revie et al., 2009). While this evidence is alarming, presently, it is not possible to accurately estimate the reduction in the smolt survival rate due to sea lice-induced mortality on a national scale as the effect varies between fjords, and from one river to another. However, according to some estimates (Anon., 2014), the effect on the smolt survival rate at the national level is considered to be larger, from 25% to 75%. As indicated, other salmon stocks, such as Pacific salmon, are also threatened by sea lice infections, and Krkosek et al. (2007) reported that lice-induced mortality of pink salmon commonly exceeded 80%. Increased sea lice densities may be considered a type of biological pollution and thus a unidirectional externality propagating from the farmed salmon sector to the wild salmon one.

According to Asche (2009), there is little doubt that aquaculture production will continue to expand, allowing the sea lice density to continue to grow as well. Due to this growing concern, in this work, we develop a wild salmon population model that can be applied to assess the economic loss due to sea lice. Because sea lice mainly infect the salmon post-smolt, while the harvest value is related to the mature spawning fish, an age-structured population model is required. The economic losses are analyzed by evaluating the reduced harvest, as well as the reduced conservation value, due to various sea lice-induced mortality scenarios. First, we analyze the case in which the wild salmon manager aims to maximize the welfare under selective harvesting of the different salmon age classes. Next, we compare this harvesting regime with a case where a uniform welfare-maximizing fishing mortality rate is imposed across the different age classes. Finally, we analyze the outcome of the manager maintaining a fixed fishing mortality rate that is not adjusted according to the sea lice-induced mortality level.

These three harvest strategies were chosen for analysis because, during the last decade, the management regime of the wild Atlantic salmon in Norway has gradually shifted from considering fish as “just a fish” towards greater focus on a selective harvesting pattern for each year class of mature salmon (Thorstad et al. 2001). This is made possible by allowing for “catch and release” management strategy, whereby the angler is supposed to release the salmon if the bag limit of that specific year class of salmon (measured by size) is met. This policy has also enabled angling for the smallest size class, fish less than 3 kg, or the so called 1SW, while mandating release of all older (larger) salmon.[1] However, this new potential management flexibility has not yet been fully implemented, and the differences in management practice between rivers are substantial. Thus, the overall aim of this paper is to assess the welfare loss due to the presence of sea lice under different scenarios, and to explore the extent to which the optimal harvesting policy is affected by sea lice-induced mortality. Therefore, we depart from the work of Liu et al. (2011b) in a number of important aspects, since we study a different salmon species, and focus on recreational instead of commercial fishery. However, the most important difference is that we consider not only harvest values, but also non-consumptive values, in addition to analyzing selective harvest of different age classes.

Fishery ecologists (e.g., Hilborn and Walters, 2001; Walters and Martell, 2004) and economists (e.g., Wilen, 1985; Townsend, 1986) have argued that management models should be based on age- / stage-structured biological models instead of the simplified biomass models. Due to the complexity of age-structured models, most of the extant economic research based on such models has basically involved case studies illustrated by numerical analysis. One noteworthy exception is the work of Tahvonen (2009), who presented analytical results pertaining to optimal harvesting under certain simplifying assumptions within a dynamic framework. Another example of a more comprehensive study is the work of Skonhoft and Gong (2014), who analyzed a salmon model with two mature (harvestable) age classes. An earlier study conducted by Skonhoft et al. (2012) is also relevant for the present investigation, as the authors analyzed a static maximum economic yield fishery with three age classes under perfect and imperfect selectivity conditions. They demonstrated several analytical results that contrast those found in the biomass models.

2. Methods

2.1 Population model

Atlantic salmon is an anadromous species with a complex life cycle that includes several phases. Freshwater habitat is essential for the early development stages, where this salmon species spends

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[1] 1SW are salmon that have stayed 1 winter (e.g. 1 sea winter) in the offshore habitat before they return to spawn in the river. Further, 2SW and 3SW have stayed 2 and 3 winters, respectively, before spawning migration.

the first 1-4 years from spawning to juvenile rearing, before undergoing smoltification and seaward migration. It spends the subsequent 1-3 years feeding and growing in the ocean. Finally, when mature, it returns to its natal, or "parent", rivers to spawn in the spring and/or summer. After spawning in autumn, most salmon die, as less than 10% of the female salmon spawn twice (Mills 1989). Atlantic salmon is subject to fishing when it migrates back to its parent river. Due to strict regulations of the marine salmon fishery that have been imposed in 2008, sea fishing has been gradually reduced, and has ceased in many fjords (Statistics Norway 2014). In the rivers, salmon are caught by recreational anglers with fishing rods. In the following sections, we assume that all harvest takes place in the river.

In what follows, a specific salmon population (with its native river) is considered in number of individuals at time t structured as recruits $N_{0,t}$ ($yr < 1$); three young age classes, $N_{1,t}$ ($1 \leq yr < 2$), $N_{2,t}$ ($2 \leq yr < 3$) and $N_{3,t}$ ($3 \leq yr < 4$); and three adult spawning classes, $N_{4,t}$ ($4 \leq yr < 5$), $N_{5,t}$ ($5 \leq yr \leq 6$), and $N_{6,t}$ ($6 \leq yr \leq 7$). Recruitment is endogenous and density-dependent, and the old spawning salmon have higher fertility than the young spawning salmon (McGinnity et al., 2003). Natural mortality is fixed and density-independent, and, in line with the work of Liu et al. (2013), we assume that the entire spawning population dies after spawning. It is further assumed that the proportion among the three mature age classes remains constant. In fixing this ratio, we imply that a given proportion of the stock returns to spawn after one, two or three years at sea, respectively (see below). A number of factors, such as type of river ("small salmon river" vs. "large salmon river") and various environmental factors (NOU, 1999) may influence these proportions. As fishing takes place when the fish return to their native river, only the mature salmon stocks $N_{4,t}$, $N_{5,t}$, and $N_{6,t}$ are subject to fishing. A detailed description of the life cycle of the Atlantic salmon can be found in Verspoor et al. (2003).

Denoting the size of the spawning population, adjusted for different fertilities among the three spawning classes (see below) as B_t, the stock recruitment relationship is first defined by:

(1) $$N_{0,t+1} = R(B_t).$$

where $R(B_t)$ may be a one-peaked value function (e.g., of the Ricker type) or it may be increasing and concave (e.g., of the Beverton-Holt or Cushing type). In both cases, zero stock implies zero recruitment, i.e., $R(0) = 0$. The number of young, depending on natural mortality, can thus be expressed as:

(2) $$N_{a+1,t+1} = s_a N_{a,t};\ a = 0,1,2,$$

where s_a is the constant age-specific natural survival rate. Finally, we have the mature age classes that are subject to fishing mortality in addition to natural mortality. With $0 < \sigma < 1$ as the proportion of the mature stock that returns to spawn the first year, the number of spawning fish of this part of the adult population (1SW) is given by:

(3) $N_{4,t+1} = s_3 N_{3,t} \sigma (1 - f_{4,t+1})$,

where $0 \leq f_4 \leq 1$ is the fishing mortality and N_3 is the pre-adult population stage. Accordingly, $H_{4,t+1} = s_3 N_{3,t} \sigma f_{4,t+1}$ is the number of harvested 1SW mature fish at year $t+1$. As indicated, the parameter σ may vary due to, for example, river type; however, here, it is considered fixed and exogenous. The remainder of this cohort, $s_3 N_{3,t}(1-\sigma)$, remains in the ocean for one or two additional years. The proportion of the mature stock that returns to spawn after the second year is given by $0 \leq \varphi \leq 1$. Moreover, since they are also subject to natural mortality as well as subsequent fishing mortality when they migrate back to the home river, the size of the next year's spawning population (2SW) becomes:

(4) $N_{5,t+2} = s_3 N_{3,t}(1-\sigma)\varphi s_4 (1 - f_{5,t+2})$,

where $0 \leq f_5 \leq 1$ is the fishing mortality and $s_3 N_{3,t}(1-\sigma)\varphi s_4 f_{5,t+2}$ is the number of harvested 2SW of this cohort year $t+2$. The remainder of this cohort, $s_3 N_{3,t}\left(1-\sigma-\varphi+\varphi\sigma\right)s_4$, stays in the ocean for one additional year. After accounting for natural mortality and subsequent fishing volume, the size of the next (third) year's spawning stock (3SW) is denoted by:

(5) $N_{6,t+3} = s_3 N_{3,t}\left(1-\sigma-\varphi+\varphi\sigma\right)s_4 s_5 (1 - f_{6,t+3})$.

where $0 \leq f_6 \leq 1$ is the fishing mortality and $s_3 N_{3,t}\left(1-\sigma-\varphi+\varphi\sigma\right)s_4 s_5 f_{6,t+3}$ is the number of harvested 3SW of this cohort year $t+3$.

Further, we denote the fecundity parameters of the small (1SW), middle (2SW), and large (3SW) mature populations by γ_4, γ_5, and γ_6, respectively. These fecundity parameters are adjusted to take into account presence of different fractions of females and males at the different stages, and to indicate that substantially more males than females enter the river after only one winter offshore (Hvidsten et al., 2004). Since the fecundity is associated with females only (McGinnity et al., 2003), the proportion of females at each stage is included (see also section 3.1 below).[2] The spawning population year t is defined as $B_t = \gamma_4 N_{4,t} + \gamma_5 N_{5,t} + \gamma_6 N_{6,t}$, or:

(6) $B_t = \gamma_4 s_3 N_{3,t-1}\sigma(1-f_{4,t}) + \gamma_5 s_3 N_{3,t-2}(1-\sigma)\varphi s_4 (1-f_{5,t}) + \gamma_6 s_3 N_{3,t-3}\left(1-\sigma-\varphi+\varphi\sigma\right)s_4 s_5 (1-f_{6,t})$.

As the fecundity parameters will be considered as dimensionless parameters, B_t is measured as the fertility-weighted number of spawning salmon. Thus, Equation (1) and (2) imply $N_{3,t+3} = s_0 s_1 s_2 N_{0,t}$, or:

(7) $N_{3,t+4} = sR(B_t)$

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[2] The implicit assumption is that there will always be a sufficient number of males at the spawning ground.

where $s = s_0 s_1 s_2$ comprises previous years survival rates. Note that the pre-adult population stage N_3 constitutes the basis for the three adult stages, N_4, N_5, and N_6 (see also Figure 1). For given fishing mortalities, Equation (7) and (6) yield a system of two difference equations of the seventh degree in the two variables $N_{3,t}$ and B_t.

The population equilibrium for fixed fishing mortalities is defined for $N_{3,t} = N_3$ and $B_t = B$ for all t such that:

(6') $$B = [\gamma_4 s_3 \sigma(1-f_4) + \gamma_5 s_3 (1-\sigma)\varphi s_4 (1-f_5) + \gamma_6 s_3 \left(1-\sigma-\varphi+\varphi\sigma\right) s_4 s_5 (1-f_6)] N_3$$

and

(7') $$N_3 = sR(B).$$

In what follows, (6') is referred to as the *spawning constraint* while (7') represents the *recruitment constraint*. An internal equilibrium ($N_3 > 0$ and $B > 0$) holds only if the values of either f_4, f_5, or f_6, or all three, are below one; that is, if depletion is to be prevented, not all mature classes can be fished to extinction.[3] The dynamics of this system for fixed fishing mortalities is found to be very stable. Thus, in the present exposition, we are only concerned with equilibrium fishing, or sustainable harvesting. While analytically deriving the stability conditions for the above system is demanding, a high degree of stability is to be expected as equation (6`) is linear, while equation (7`) is concave as long as the recruitment function is concave. This observation is confirmed by numerical simulations. However, to ensure an internal unique solution, we must ensure that the slope of the spawning constraint (6`), when $N_3$ is measured along the horizontal axis, is less steep than the slope of recruitment constraint (7`) as the stock converges to zero (see Skonhoft and Gong (2014) for a dynamic analysis of a slightly different model).

Since the mortality of wild salmon is influenced by the sea lice on the seaward migration of the smolt only, the survival rate s in Equation (7') is the only parameter that is affected by the sea lice density. Therefore, we can study the lice problem in our model by assessing harvest and stock effects of changing the values of this parameter. For fixed fishing mortalities, a greater lice density and lower survival rate s will reduce the size of the spawning population as well as the population size N_3 through Equation (6') and (7'). On the other hand, when optimizing the fishing, these effects will be counterbalanced to some extent by changing fishing mortalities. The magnitudes of these effects are analyzed in section 3 below.

2.2 The benefit of wild salmon

Atlantic salmon has both use and non-use value, or harvest and conservation value, respectively. The benefit from recreational harvest is represented by the utility function $U(Y)$, where Y is the year class scaled biomass harvested (in NOK) per year. Here, we denote the fixed weights (kg per

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[3] As indicated above, e.g., $f_4 = 1$ does not imply stock depletion in this model, as this only means that the entire 1SW proportion of the stock is fished down.

fish) of the 1SW, 2SW, and 3SW mature population as w_4, w_5, and w_6, respectively, where $w_6 > w_5 > w_4$. Thus, the biomass harvested (in kg) is first defined by $y = w_4 s_3 \sigma f_4 N_3 + w_5 s_3 (1-\sigma)\varphi s_4 f_5 N_3 + w_6 s_3 \left(1-\sigma-\varphi+\varphi\sigma\right) s_4 s_5 f_6 N_3$. The utility obtained from different year classes may typically differ. For example, recreational anglers may prefer harvesting 3SW salmon relative to 2SW salmon, and 2SW over 1SW, due to the trophy aspect of the fishing experience (see Nævdal et al., 2012). Thus, to allow for different preferences for different age classes, we introduce the scaling parameter $z_i\,(i = 4,5,6)$ (in NOK/kg) for each of the year classes in the harvest, where we typically have $z_6 \geq z_5 \geq z_4$ (Olaussen and Liu, 2011). Now, the year class-scaled biomass value harvested (in NOK) can be written as: $Y = z_4 w_4 s_3 \sigma f_4 N_3 + z_5 w_5 s_3 (1-\sigma)\varphi s_4 f_5 N_3 + z_6 w_6 s_3 \left(1-\sigma-\varphi+\varphi\sigma\right) s_4 s_5 f_6 N_3$, where the scaling parameters introduce the only difference compared to y defined above.

The conservation-related benefit is defined by the utility function $V(Q)$, where $Q = w_4 s_3 \sigma (1-f_4) N_3 + w_5 s_3 (1-\sigma)\varphi s_4 (1-f_5) N_3 + w_6 s_3 \left(1-\sigma-\varphi+\varphi\sigma\right) s_4 s_5 (1-f_6) N_3$ represents the stock (in kg) after harvest has taken place. A pure non-use value is also called existence value, and reflects the fact that people are willing to pay for improving or preserving resources they will never use (Perman et al., 2011). In our case, it indicates that many individuals place value on the existence of wild salmon even if they never go, or intend to go, fishing. The value is simply associated with the mere knowledge that this valuable natural resource exists. Both $V(Q)$ and $U(Y)$ are assumed to be increasing and concave functions, implying that both higher salmon stock and higher harvest yield more utility, albeit at a decreasing degree.

The sustainable social welfare function taking both the conservation and the use perspective of salmon into account (see Liu et al., 2013) can be expressed as $W = W\left[U(Y), V(Q)\right]$. Thus, assuming separability, it can be denoted as:

$$W = \alpha\left[U(Y)\right] + (1-\alpha)\left[V(Q)\right]. \tag{8}$$

Here, the parameter $0 \leq \alpha \leq 1$ is a weighting factor between the harvest and conservation values. Hence, when $\alpha = 1$, the welfare function accounts for harvest only, while $\alpha = 0$ implies that only the conservation value is considered. Finally, $\alpha = 0.5$ indicates similar valuation of harvest (in NOK) and stock abundance (in kg).

2.3 Management strategies

To reduce the effect of recreational angling on fish stocks, "catch and release" programs have been implemented in many Atlantic salmon rivers, especially in North America. In Norway, "catch and release" is practiced on a voluntary basis, and also as a management tool to protect certain size groups in some rivers (Thorstad et al., 2001). Moving from a strict number-based bag limit (e.g., one salmon per angler per day) to a size-grouped bag limit (e.g., one 1SW per day) is only possible by allowing "catch and release", since recreational angling fishing gear (rod fishing) is non-selective by nature.

The maximum sustainable social yield problem with separate fishing mortalities for the three harvestable year classes is described by finding fishing mortalities that maximize the equilibrium social welfare function (8) subject to the spawning constraint (6') and the recruitment constraint (7'). The Lagrangian of this problem can be expressed as:

$$
\begin{aligned}
L = {} & \alpha[U\left((z_4 w_4 s_3 \sigma f_4 + z_5 w_5 s_3 (1-\sigma)\varphi s_4 f_5 + z_6 w_6 s_3 \left(1-\sigma-\varphi+\varphi\sigma\right) s_4 s_5 f_6) N_3\right)] \\
& +(1-\alpha)\left[V\left((w_4 s_3 \sigma (1- f_4) + w_5 s_3 (1-\sigma)\varphi s_4 (1- f_5) + w_6 s_3 \left(1-\sigma-\varphi+\varphi\sigma\right) s_4 s_5 (1- f_6)) N_3\right)\right] \\
& -\lambda[N_3 - sR(B)] \\
& -\mu\{B - [\gamma_4 s_3 \sigma (1- f_4) + \gamma_5 s_3 (1-\sigma)\varphi s_4 (1- f_5) + \gamma_6 s_3 \left(1-\sigma-\varphi+\varphi\sigma\right) s_4 s_5 (1- f_6)] N_3\} \qquad ,
\end{aligned}
$$

where $\lambda > 0$ and $\mu > 0$ are the shadow values of the recruitment and spawning constraints, respectively. The first order optimality conditions are presented in online supplement A.

For a positive spawning population, the control conditions (A1)-(A3) (see Appendix A) may be written as:

(9) $w_4 / \gamma_4 \overset{\geq}{\underset{<}{-}} \mu / [\alpha U'(.) z_4 - (1-\alpha) V'(.)]$; $0 \leq f_4 \leq 1$,

(10) $w_5 / \gamma_5 \overset{\geq}{\underset{<}{-}} \mu / [\alpha U'(.) z_5 - (1-\alpha) V'(.)]$; $0 \leq f_5 \leq 1$,

and

(11) $w_6 / \gamma_6 \overset{\geq}{\underset{<}{-}} \mu / [\alpha U'(.) z_6 - (1-\alpha) V'(.)]$; $0 \leq f_6 \leq 1$.

The interpretation of these control conditions provides some clear intuition about the optimal harvest patterns. To explore this phenomenon further, let us assume that recreational fishermen are indifferent with respect to which year class they harvest; that is, $z_4 = z_5 = z_6$. In this case, the right hand sides of these conditions are identical. Thus, only the biomass/fecundity ratio w_i / γ_i ($i = 4, 5, 6$) affects the fishing mortality and the fishing composition, and hence no other factors play a *direct* role. This outcome differs from the findings reported by Reed (1980) and Skonhoft et al. (2012), who indicated that a combination of weight and natural mortality directly determined the fishing composition. As already noted, this discrepancy stems from the different biological characteristics of the fish stocks. More specifically, in our salmon model, it is assumed that the mature fish dies after spawning. On the other hand, in these alternative models, a certain fraction of other fish (e.g., cod) survives and enters older age classes.

Generally, under the assumption of $z_4 = z_5 = z_6$, the above first order conditions (9) – (11) lead to thirty potential harvest patterns. For example, when $w_4 / \gamma_4 > w_6 / \gamma_6 > w_5 / \gamma_5$, which is in accordance with our Norwegian wild salmon data (see section 3 below), there will be five potential harvest cases, described by (i) $f_4 = 1,\ f_6 = 1,\ 0 < f_5 < 1$, (ii) $f_4 = 1,\ f_6 = 1,\ f_5 = 0$, (iii) $f_4 = 1,\ 0 < f_6 < 1,\ f_5 = 0$, (iv) $f_4 = 1,\ f_6 = 0,\ f_5 = 0$, and (v) $0 < f_4 < 1,\ f_6 = 0,\ f_5 = 0$.[4] Clearly, the most aggressive harvest pattern is represented by case

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[4] The twenty-five remaining possibilities are found by under the various assumptions $w_4 / \gamma_4 > w_5 / \gamma_5 > w_6 / \gamma_6$, $w_5 / \gamma_5 > w_6 / \gamma_6 > w_4 / \gamma_4$, $w_5 / \gamma_5 > w_4 / \gamma_4 > w_6 / \gamma_6$, $w_6 / \gamma_6 > w_5 / \gamma_5 > w_4 / \gamma_4$, and $w_6 / \gamma_6 > w_4 / \gamma_4 > w_5 / \gamma_5$.

(i), where the entire 1SW and 3SW sub-populations are harvested, while the subsequent cases are progressively less aggressive. Hence, case (v) represents the lowest harvesting pressure, where it is optimal to harvest only some proportion of the 1SW. Note that the sea lice has no direct effect on these optimal control conditions through s. Hence, the sea lice-induced mortality indirectly affects the optimal harvest pattern through the size of the harvestable population and the stock sizes only. However, as we find that more lice and lower survival rate s reduces the harvestable population (section 2.1), we suspect that greater presence of lice will lead to less aggressive harvesting. Therefore if, say, the above case (i) initially describes the optimal harvest pattern, reduced survival may lead to retaining this harvest pattern. On the other hand, with a reduction in f_5, it may change to the less aggressive case (ii), or any other of those shown above.

The optimal selective harvest pattern described above may be compared to the outcome of allowing fishing to take place in a uniform manner; that is, fishing mortality is similar among all three harvestable classes. For example, as already indicated, this scenario would occur if "catch and release" fishing is forbidden for ethical reasons, since the fishing gear is non-selective. In this case, our economic problem aims to maximize the sustainable social welfare, subject to the biological constraints (6') and (7') *and* the restriction that the same fishing mortality is imposed for all harvestable classes, i.e., $f_4 = f_5 = f_6$. The first order optimality conditions of this problem are shown in online supplement B. Again, while the sea lice have no direct effect through the optimal control conditions, we may still suspect that higher mortality will lead to less aggressive fishing.

In addition to the two optimizing regimes described above, we will also examine a management regime in which the baseline optimal uniform harvest rate is maintained at a constant level under different sea lice-induced mortality scenarios, indicating that the manager does not respond to shifting biological conditions. This harvest regime may reflect a situation in which "catch and release" strategy is not allowed and the manager keeps regulations unchanged due to either ignoring the smolt survival and/or lack of knowledge. Note that this is also one of the harvest regimes considered in Liu et al. (2011b).

3. Results

3.1 Data and functional forms

The theoretical reasoning delineated above will now be illustrated numerically. Hansen et al. (1996) estimated a salmon recruitment function for a small river in Norway (the Imsa River, located in the southern part of Norway) based on the Shepherd stock-recruitment function that includes three parameters. In line with Norwegian salmon data, here, we apply the Cushing version of this function specified as $R(B) = r\dfrac{B}{1+(B/K)^{\eta}}$ with $r > 0$ as the intrinsic growth rate (maximum number of recruits per fertility adjusted spawner), $K > 0$ (number of spawners) as the stock level for which density dependent mortality equals density independent mortality, and η as the curvator of the density dependence. The size of rK is scaling the system ("size of the river"), and is assumed to be 40.000 (number of recruits). The value of r indicates the "quality" of the river, and is set at $r = 400$, yielding $K = 100$. The natural survival rate of the young *in absence* of sea lice introduced through aquaculture is assumed to be 5%, $s = 0.05$, and is hence our reference value for assessing the welfare loss. This survival rate, as well as the ones for the adults, is based on the work of NOU (1999) and Hvidsten et al. (2004).

Table 1 shows these values, along with all other baseline parameter values used in the numerical analysis. When using the fertility-weight function of McGinnity et al. (2003) together with the female/male shares for the different mature stages adopted from Hvidsten et al. (2004), we find $\gamma_4 = 1.72$ $\gamma_5 = 9.3$, and $\gamma_6 = 12.19$ under the assumption of (average) fishing weights $w_4 = 2.1$, $w_5 = 5.1$, and $w_6 = 9.0$ (kg/salmon) (Hvidsten et al., 2004). Therefore, for the given weight and fecundity values, the weight–fertility ratio is higher for the 1SW stage compared to the 3SW, which is again higher than that pertaining to 2SW; that is, $w_4 / \gamma_4 > w_6 / \gamma_6 > w_5 / \gamma_5$. Note that the weight and fecundity rates do not follow the pattern we would expect under a concave fecundity-weight relationship ($w_6 / \gamma_6 > w_5 / \gamma_5 > w_4 / \gamma_4$) because of the different male/female ratios in the populations found in the different stages.[5] In the calculations presented, we assume the same fishing valuation of the old, middle and young mature age classes; hence, $z_1 = z_2 = z_3$. The scaling parameters z_i are calibrated in order to coincide with a harvest value of about NOK 800 on average per harvested salmon in the baseline scenario.[6] The prices are calculated based on the recreational fishing permit prices. The assumption here is that the fishing permit price in a typical salmon river may be about NOK 200 per day.[7] Based on an average catch success, this permit price corresponds to a per kg fish price of NOK 250 (NOK/kg),[8] which is reflected by the z_i parameters in the utility function. Finally, the social welfare function is specified by the logarithmic form, $W = \alpha \ln Y + (1-\alpha) \ln Q$, and thus implies a relative welfare loss aversion coefficient of one for harvest as well as conservation.

3.2 Selective harvest results

3.2.1 Managing for harvest value only, $\alpha = 1$

First, we look at the harvest pattern with perfect selective fishing, as described by conditions (9) – (11), assuming that the manager is concerned with the use value (harvest value) only. With

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[5] Following McGinnity et al. (2003), the fecundity of returning females is given by the concave function $F = cW^k$ where c=4.832, k =0.8697, and W is weight in grams of spawning female. Hence, for the given weights (main text above) for 1SW, 2SW and 3SW salmon, fecundities are found to be 9.212, 13.61 and 19.956, respectively. Then, when adjusting for the share of females at each stage, that is, 1SW=(1-m_1)=0.187, 2SW=(1-m_2)=0.683, and 3SW=(1-m_3)=0.611, where m_1, m_2, and m_3 are male shares, respectively (see Table 1) (Hvidsten et al., 2004), we have $\gamma_4 = 1.72$, $\gamma_5 = 9.3$, and $\gamma_6 = 12.19$.

[6] Exploration of sensitivity with respect to different preferences for different stages (different values of the z_i parameters) and their effects on the harvesting patterns is postponed to later research, as we are not aware of any empirical data to support calibration of these parameters. However, simulation of changes in the range of less than 10 percent does not seem to influence the harvest patterns.

[7] Olaussen and Skonhoft (2008) use NOK 200. However, the variation among different rivers is large and is found to vary from NOK 50 to NOK 200,000 (Liu et al., 2011a). Based on the average permit prices in small, medium and large rivers in the 2012 season, NOK 200 seems to be a reasonable estimate.

[8] Average catch per unit effort (CPUE) is 0.26 (fish/fishing day) (Tangeland et al., 2008). Average size of salmon caught in Norwegian rivers in 2010 was 3.3 kg (Statistics Norway 2013). Hence, the average price per kg is 200NOK/(0.26*3,1 kg)=250 NOK/kg.

weight–fertility variations given as $w_4 / \gamma_4 > w_6 / \gamma_6 > w_5 / \gamma_5$ and $z_4 = z_5 = z_6$ (Table 1), the potential optimal fishing mortality possibilities are given by cases (i) – (v), as shown in section 2.2. As noted in section 1, the sea lice-induced effect arising from salmon aquaculture on smolt mortality varies from 25% to 75%. To take this variation into account, we assess the consequences at different sea lice-induced mortality levels (Table 2). In the baseline scenario without sea lice, when $s = 0.05$ (see Table 2, first row), we find that case (i) with $f_4 = f_6 = 1$ and $f_5 = 0.51$ describe the optimal fishing mortality pattern. When smolt mortality increases and s reduces to $s = 0.02$ (implying 60% smolt survival reduction), fishing becomes less aggressive and 2SW mortality reduces, while it is still optimal to maintain $f_4 = f_6 = 1$. With this survival rate, the social welfare is reduced by 19%, from 6.083 to 4.916. In addition, with 80% reduction in the smolt survival ($s = 0.01$), the fishing mortality f_5 is reduced to zero, resulting in the harvest pattern (ii) described in section 2.2. In this case, the social welfare is reduced by about 36% when compared with the baseline scenario. Note that the welfare loss in general is relatively small compared to the changes in harvest and stock size. This phenomenon is due to the concavity of the utility functions, which also explain why welfare and utility reductions are greater at low stock and harvest levels.

3.2.2 Managing for harvest and conservation value, $\alpha = 0.5$

When the manager assigns equal importance to both the harvest and the conservation value, the optimal harvest pattern becomes less aggressive (Table 3). In the baseline case without sea lice mortality, harvest pattern (iii) (section 2.3 above) with $f_4 = 1,\ f_6 = 0.27,$ and $f_5 = 0$ now describes the optimal fishing mortalities. If natural mortality is reduced by 80% due to sea lice infestation (s =0.01), the harvest pattern (iv) with $f_4 = 1,\ f_6 = 0,$ and $f_5 = 0$ become the most optimal. Finally, a further reduction of the natural mortality, s =0.005, yields the case (v) with $f_4 = 0.88,\ f_6 = 0,$ and $f_5 = 0$. However, it should be noted that, while the harvest of 2SW and 3SW is below the levels obtained when only the harvest value is considered by the manager (Table 2), the 1SW is actually harvested at a higher rate when the conservation value is taken into account. This outcome is a direct effect of the desire to keep a higher stock when conservation value is given due importance. When the stock is higher, and the fertility/weight relationship remains unchanged, it is still optimal to harvest the entire 1SW population. Consequently, the resulting number of harvested 1SW salmon becomes higher. On the other hand, the welfare reduction due to sea lice-induced mortality is always less pronounced than when only harvest values are considered. For example, if the natural mortality is reduced by 80% (s =0.01), the social welfare is reduced by about 30% in this case, compared to 36% in the harvest value case above.

3.3 Non-selective harvest results

3.3.1 Uniform harvest pattern, managing for harvest value only, $\alpha = 1$

Table 4 reports the outcome when the stock is harvested through a uniform harvest pattern, as described at the end of section 2.3, and the manager is only concerned with the harvest value. As expected, the optimal uniform fishing mortality is gradually reduced when the smolt survival decreases due to the sea lice-induced mortality. However, somewhat surprisingly, we find that a 20% reduction in the survival rate (s =0.04) results in only a rather modest reduction in the fishing mortality; from 0.80 to 0.78 (3%). Moreover, a 60% reduction in the survival rate ($s = 0.02$) leads to a 13% reduction in the fishing mortality, while the harvest and social welfare are reduced by 71% and 20%, respectively. It should also be noted that, compared to the selective fishing case (Table 2), the difference in social welfare is quite modest. This finding simply indicates that the welfare gain of perfect fishing selectivity versus uniform fishing is quite modest for all levels of sea lice-induced mortality.

3.3.2 Uniform harvest pattern, managing for harvest and conservation value, $\alpha = 0.5$

Table 5 reports the outcomes of a scenario in which the manager assigns equal importance to the harvest value and the conservation value. Not surprisingly, in this case, the harvest rate is reduced significantly compared to the situation represented in Table 4, where the manager is only concerned with the harvesting utility. More specifically, the baseline value now declines to just 0.45. However, as above, the fishing mortality is quite insensitive to higher sea lice-induced mortality, and reducing the natural survival by 60% (s =0.02) only reduces the fishing mortality to 0.41 (i.e., by about 9%). In this situation, social welfare is reduced by about 17% (from 6.391 to 5.333). In addition, the welfare loss associated with uniform harvest compared to selective harvest is less pronounced when the conservation value is taken into account than when only harvest is considered. For example, with s =0.02, the social welfare difference is only about 1%, and even in the most severe sea lice-induced mortality case (s =0.005), the welfare loss associated with uniform harvest is only 4% (see Table 3). This smaller difference in welfare is directly related to the fact that, relative to stock size, harvest is less important. Hence, the type of harvest composition is also less important.

3.3.3 Fixed uniform harvest pattern, managing for harvest value only, $\alpha = 1$

Table 6 presents the results obtained when the optimal baseline uniform harvest rate $f_4 = f_5 = f_6 = 0.80$ is kept constant and only the harvest value is taken into account. These calculations hence yield stock changes and the accompanying utility losses when the lice-induced smolt mortality rate increases without any adjustment to the harvesting pattern. As can be seen, compared to the scenario in which the uniform harvest rate is chosen optimally (Table 4 and 5), the losses of maintaining a fixed harvest rate are rather modest, provided that the sea lice-induced mortality is not too strong. For example, while the utility is reduced by 19% when the harvest is adjusted and the mortality changes from $s = 0.05$ to $s = 0.02$ due to sea lice (Table 4), it is reduced by 22% in the unadjusted case (Table 6). However, when the smolt survival rate is reduced by more than 80% ($s < 0.01$), this fixed harvest rate regime leads to population extinction, whereby all the salmon utility ceases. In other words, even when the recruitment function is steep, when the fishing mortality is fixed at 0.8, the total mortality (sea lice-induced mortality, natural mortality, and fishing mortality) is simply too high to recruit the river.

4. Discussion and conclusion

We have analyzed one example of the more general class of problems where man-made activities lead to negative effects on species. The overall aim was to analyze how the harvest regimes and social welfare obtained from wild Atlantic salmon may change when an external factor, exemplified by increased sea lice density associated with salmon aquaculture production, increases mortality and reduces the size of the wild salmon spawning populations. In contrast to the present harvest regime in Norwegian salmon rivers, our study shows that it is always optimal to harvest the entire 1SW subpopulation when it is possible to select perfectly between the harvestable year classes. Our finding is based on the fact that the biomass-value/fecundity relationship is higher for 1SW than for the other two mature classes when the sex bias of the different population sizes is taken into account. In addition, the presence of the other two stages is sufficient to secure recruitment. We thus demonstrate that fishing according to a uniform harvest pattern, without allowing for different harvest rates among the various age classes, considerably reduces the utility only when the sea lice-induced mortality is very high. Moreover, the consequences of applying a uniform harvest rate regime are less pronounced if conservation values are also taken into account by the manager. However, it should be noted that the above analysis neglected discounting. It has been shown that discounting would have the expected effect of inducing more aggressive harvest in the case when the focus is solely on harvest value (see Skonhoft and Gong, 2014); however, it is likely that the harvest composition would not change considerably.

Table 7 summarizes the results of a 60% reduction in the smolt survival rate, along with the comparison with the baseline survival rate; that is, the survival rate in absence of sea lice-induced mortality arising from salmon aquaculture. This 60% reduction, $s = 0.02$, may represent the typical survival rate in many Norwegian rivers due to the high sea lice densities associated with aquaculture. The salmon stock reduction varies from 64% to 74% in the different scenarios considered here. The harvest is generally reduced slightly more than the stock, and is within the 65% − 74% range. In contrast, the consequence for the welfare reduction ranges from 16% to 22%. This finding indicates that, when the manager is solely focused on the welfare consequences, rather dramatic external threats may not be treated with the necessary caution, since the welfare effect is quite modest compared to the stock effect. The quite modest welfare changes are explained by decreasing marginal utility both with respect to harvest and non-consumptive values. Even in a case of a small salmon population, the recreational utility may be quite high due to the mere fact that it is possible to keep fishing. In the same vein, the non-consumptive/conservation value is severely reduced primarily when the stock levels approach extinction threshold. Hence, when considering the conservation value, the difference between a high and a very high population may not be of particular importance, while the difference between a low and a very low stock may be substantial.

The potential conflict between utilization and conservation of renewable resources is important, in particular when external factors influence the resource abundance negatively. This leads to the issue of determining the extent to which the external threat changes the management of the actual natural resource, and hence how the balance between use and conservation may be influenced. Our results indicate that increased sea lice density does not necessarily call for altered harvest regimes. In other words, changing the harvest priority among the harvestable age classes may not be not required, particularly when the increased mortality rate from sea lice infection is small and modest. In fact, we find surprisingly aggressive harvest patterns to be persistent even in very high sea lice-induced mortality scenarios. However, under a fixed uniform fishing mortality condition, high sea lice-induced mortality may drive the population to extinction. This result is consistent with the findings reported by Liu et al (2011b), who have shown that, under a fixed harvest rate regime, the pink and chum salmon populations may collapse at high sea lice-induced mortality rates. Thus, an optimal selective harvesting regime should be employed to secure both the highest potential welfare and a viable population.

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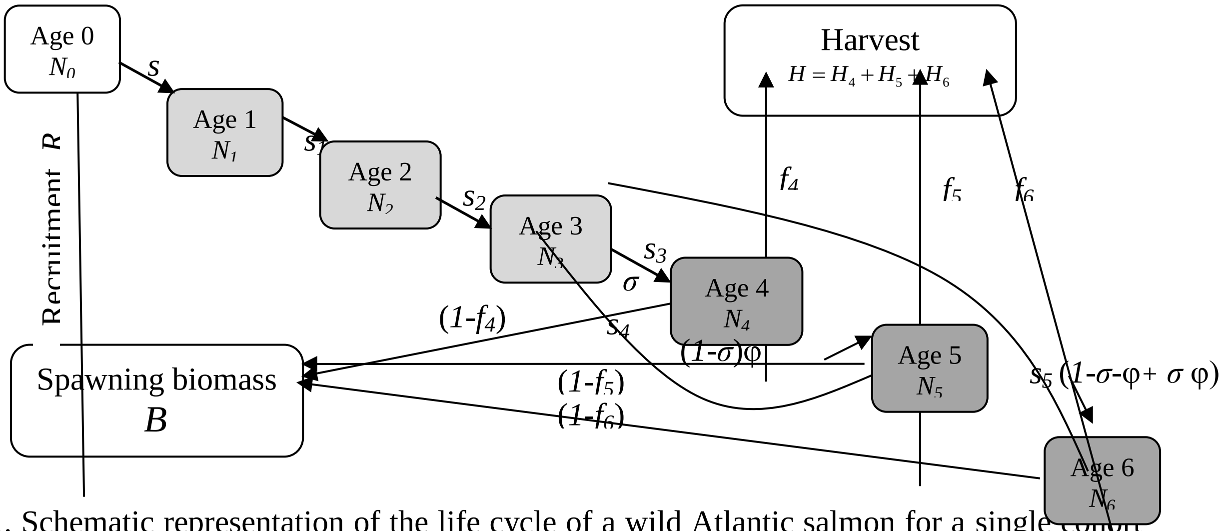

Figure 1. Schematic representation of the life cycle of a wild Atlantic salmon for a single cohort (the time index is omitted). See main text for definition of symbols.

Table 1. Biological and economic baseline parameter values

Parameter	Description	Value
s	Natural survival rate young without sea lice induced mortality	0.05
s_3	Natural survival rate 1SW	0.5
s_4	Natural survival rate 2SW	0.5
s_5	Natural survival rate 3SW	0.5
r	Intrinsic growth rate recruitment function	400 (# of recruits/ fertility adjusted spawner)
K	Scaling parameter recruitment function	100 (# of spawners)
η	Curvator of density dependence recruitment function	0.96
σ	Migration parameter 1SW	0.43
φ	Migration parameter 2SW	0.55
w_4	Weight 1SW	2.1 (kg/fish)
w_5	Weight 2SW	5.1 (kg/fish)
w_6	Weight 3SW	9.0 (kg/fish)
m_1	Male share 1SW	0.813
m_2	Male share 2SW	0.317
m_3	Male share 3SW	0.389
γ_4	Fecundity parameter 1SW	1.72
γ_5	Fecundity parameter 2SW	9.3
γ_6	Fecundity parameter 3SW	12.19
z_4	Scaling value 1SW	0.250 (1000NOK/kg)
z_5	Scaling value 2SW	0.250 (1000NOK/kg)
z_6	Scaling value 3SW	0.250 (1000NOK/kg)

Sources: See main text

Table 2: Managing for harvest value only ($\alpha = 1$). Optimal selective fishing mortalities under different sea lice-induced mortality levels.

	f_4	f_5	f_6	N_3	H_4	H_5	H_6	U	V	W
s=0.05	1	0.51	1	1883	400	74	60	6.083	5.905	6.083
s=0.04	1	0.46	1	1446	311	52	46	5.811	5.743	5.811
s=0.03	1	0.38	1	1041	224	31	33	5.447	5.553	5.447
s=0.02	1	0.26	1	647	139	13	21	4.916	5.254	4.916
s=0.01	1	0	1	270	58	0	9	3.911	4.681	3.911
s=0.005	1	0	0.44	94	20	0	1	2.610	3.966	2.610

Note: f_4 , f_5 and f_6 are harvest rates for the 1SW, 2SW and 3SW class, respectively. N_3 is the pre-adult stage population. H_4 , H_5 , and H_6 are the harvest (# of salmon) of the 1SW, 2SW, and 3SW, respectively, while U is the utility in the recreational fishery, V is the non-consumptive utility and W is the weighted social welfare. s is the lumped survival rate from the juvenile to the smolt stage where $s=0.05$ is the survival rate in absence of sea lice due to aquaculture.

Table 3: Managing for harvest and non-consumptive values ($\alpha = 0.5$). Optimal selective fishing mortalities under different sea lice-induced mortality levels.

	f_4	f_5	f_6	N_3	H_4	H_5	H_6	U	V	W
s=0.05	1	0	0.27	2151	462	0	18	5.651	7.185	6.418
s=0.04	1	0	0.25	1683	362	0	13	5.395	6.944	6.140
s=0.03	1	0	0.22	1221	263	0	9	5.058	6.637	5.847
s=0.02	1	0	0.15	767	165	0	4	4.553	6.204	5.378
s=0.01	1	0	0	327	70	0	0	3.608	5.416	4.512
s=0.005	0.88	0	0	115	22	0	0	2.436	4.447	3.441

Note: f_4 , f_5 and f_6 are harvest rates for the 1SW, 2SW and 3SW class, respectively. N_3 is the pre-adult stage population. H_4 , H_5 , and H_6 are the harvest (# of salmon) of the 1SW, 2SW, and 3SW, respectively, while U is the utility in the recreational fishery, V is the non-consumptive utility and W is the weighted social welfare. s is the lumped survival rate from the juvenile to the smolt stage where $s=0.05$ is the survival rate in absence of increased sea lice levels due to aquaculture

Table 4: Managing for harvest value only ($\alpha = 1$). Optimal uniform fishing mortality under different sea lice-induced mortality levels.

	f_4	f_5	f_6	N_3	H_4	H_5	H_6	U	V	W
s=0.05	0.80	0.80	0.80	1781	306	112	46	6.006	6.006	6.006
s=0.04	0.78	0.78	0.78	1378	231	84	34	5.724	5.845	5.724
s=0.03	0.75	0.75	0.75	985	159	58	214	5.349	5.637	5.349
s=0.02	0.70	0.70	0.70	603	91	33	14	4.790	5.329	4.790
s=0.01	0.58	0.58	0.58	245	31	11	5	3.701	4.765	3.701
s=0.005	0.41	0.41	0.41	85	7	3	1	2.296	4.046	2.296

Note: f_4, f_5 and f_6 are harvest rates for the 1SW, 2SW and 3SW class, respectively. N_3 is the pre-adult stage population. H_4, H_5, and H_6 are the harvest (# of salmon) of the 1SW, 2SW, and 3SW, respectively, while *U* is the utility in the recreational fishery, *V* is the non-consumptive utility and *W* is the weighted social welfare. s is the lumped survival rate from the juvenile to the smolt stage where $s=0.05$ is the survival rate in absence of increased sea lice levels due to aquaculture.

Table 5: Managing for harvest and non-consumptive values ($\alpha = 0.5$). Optimal uniform fishing mortality under different sea lice-induced mortality levels.

	f_4	f_5	f_6	N_3	H_4	H_5	H_6	U	V	W
s=0.05	0.45	0.45	0.45	2104	204	74	30	5.598	7.185	6.391
s=0.04	0.44	0.44	0.44	1642	155	57	23	5.327	6.955	6.141
s=0.03	0.43	0.43	0.43	1186	110	40	16	4.979	6.647	5.813
s=0.02	0.41	0.41	0.41	739	65	24	10	4.458	6.208	5.333
s=0.01	0.35	0.35	0.35	309	23	8	3	3.456	5.418	4.437
s=0.005	0.26	0.26	0.26	110	6	2	1	2.098	4.530	3.314

Note: f_4, f_5 and f_6 are harvest rates for the 1SW, 2SW and 3SW class, respectively. N_3 is the pre-adult stage population. H_4, H_5, and H_6 are the harvest (# of salmon) of the 1SW, 2SW, and 3SW, respectively, while *U* is the utility in the recreational fishery, *V* is the non-consumptive utility and *W* is the weighted social welfare. s is the lumped survival rate from the juvenile to the smolt stage where $s=0.05$ is the survival rate in absence of increased sea lice levels due to aquaculture.

Table 6: Managing for harvest value only ($\alpha = 1$). Fixed uniform fishing mortality under different sea lice-induced mortality levels.

	f_4	f_5	f_6	N_3	H_4	H_5	H_6	U	V	W
s=0.05	0.80	0.80	0.80	1781	306	112	46	6.006	6.006	6.006
s=0.04	0.80	0.80	0.80	1336	230	84	34	5.719	5.719	5.719
s=0.03	0.80	0.80	0.80	899	155	56	23	5.323	5.323	5.323
s=0.02	0.80	0.80	0.80	471	81	30	12	4.674	4.674	4.674
s=0.01	0.80	0.80	0.80	60	10	4	2	2.616	2.616	2.616
s=0.005	0.80	0.80	0.80	0	0	0	0	0	0	0

Note: f_4, f_5 and f_6 are harvest rates for the 1SW, 2SW and 3SW class, respectively. N_3 is the pre-adult stage population. H_4, H_5, and H_6 are the harvest (# of salmon) of the 1SW, 2SW, and 3SW, respectively, while U is the utility in the recreational fishery, V is the non-consumptive utility and W is the weighted social welfare. s is the lumped survival rate from the juvenile to the smolt stage where $s=0.05$ is the survival rate in absence of increased sea lice levels due to aquaculture.

Table 7: Summarizing stock, harvest, and welfare reduction with sea lice induced mortality of $s = 0.02$ compared with the baseline in absence of sea lice and $s = 0.05$.

	Optimal fishing mortality. Managing for harvest value only (Table 2)	Optimal fishing mortality. Managing for harvest and non-consumptive values (Table 3)	Optimal uniform fishing mortality. Managing for harvest value only (Table 4)	Optimal uniform fishing mortality. Managing for harvest and non-consumptive values (Table 5)	Fixed uniform fishing mortality. Managing for harvest value only (Table 6)
Reduced stock	1236 (66%)	1384 (64%)	1178 (66%)	1365 (65%)	1310 (74%)
Reduced harvest	363 (68%)	311 (65%)	326 (70%)	209 (68%)	341 (74%)
Reduced welfare	1.17 (19%)	1.04 (16%)	1.22 (20%)	1.06 (17%)	1.33 (22%)

Note: Stock and harvest reduction in # of salmon, percentage reduction in parenthesis.