

Wild salmon harvest with farmed salmon induced mortality

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Abstract: Recently, increased sea lice densities caused by salmon farming have received growing attention in the main producer countries Canada, Chile and Norway. This paper presents a bioeconomic model for wild Atlantic salmon on the basis of the actual sea lice problem in Norway and explores the extent to which the optimal harvest pattern is affected by sea lice induced mortality. Because the salmon post smolts are the most vulnerable to attack by salmon sea lice, while harvest value is related to the mature spawning fish, an age structured population model is required. The economic losses are analyzed by calculating the reduced harvesting value of the mature salmon due to various sea lice induced mortality scenarios. We compare the situation in which the harvest activity is assumed *not* to be influenced by sea lice with the case where the manager maximizes the sustainable harvesting value taking sea lice induced mortality into account.

JEL Codes: Q22, Q26

Key words: Atlantic salmon, sea lice, age structured model, maximum sustainable yield harvest, economic loss

1. Introduction

Man-made activities or actions often provide challenges for both terrestrial as well as aquatic species. The most well-known examples are pollution, deforestation, habitat degradation, and introduction of invasive species. Atlantic salmon (*Salmo salar*) 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: 9; Liu et al. 2011). Aquaculture influences the wild population mainly through two channels: escaped farmed salmon and by increased 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 cause genetic interactions with the wild populations, as analyzed by Liu et al. (2012), while the sea lice problem is taken up here.

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 a problem in both the Atlantic and Pacific Oceans, while the Chilean farming industry experiences challenges with *Caligus teres* and *Caligus rogercresseyi* (Revie et al. 2009). The lice are mainly a problem for the salmon post smolt on their out-migration journey, as they have to pass the fish farms before they reach their offshore winter habitat. A recent report from the scientific advisory board for salmon management in Norway states that the high sea lice densities together with escaped farmed salmon from aquaculture are the two most significant and existential threats to the wild salmon populations in Norway (Anon 2011). 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 magnitude of 100 (Heuch et al. 2005). Smolt infected by less than 10 sea lice are considered to be unaffected by the parasite. Recent evidence, however, seems to suggest that this is a threshold level such that only smolt with 10 lice or fewer survive (Heuch et al. 2005; Holst et al. 2003). In some cases, surveillance have discovered up to 100 sea lice per fish, which cause certain death (Revie et al. 2009). As indicated, other salmon stocks, such as Pacific salmon, are also threatened by sea lice infections, and Krkosek et al. (2007) found a lice induced mortality for pink salmon commonly exceeding 80%.

In this paper we formulate a wild salmon population model to assess the economic loss of the sea lice problem. Because the sea lice mainly infect the salmon post smolts, while the harvest value is related to the mature spawning fish, an age structured population model is required to capture these effects properly. The economic losses and effects on the fishing mortalities are analyzed by obtaining the reduced harvesting value of the mature salmon due to various sea lice induced mortality scenarios. First, we analyze what happens when the wild salmon manager aims to maximize the sustainable harvesting value of the wild stock under selective harvesting of the different age classes. Then, in a next step, we analyze the situation in which a uniform fishing mortality rate is applied across the different age classes. Finally, we compare these harvesting regimes with the situation in which we assume a fixed fishing mortality rate that is not influenced by reduced survival of the salmon stock due to increased sea lice density.

The reason for analyzing these three different harvest strategies is that, during the last decade, the management regime of the wild Atlantic salmon in Norway has gradually shifted from one in which a fish is considered “just a fish” towards one with 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; that is, a regime in which the angler can release the salmon if the bag limit for that specific year class of salmon (measured by size) is met. This has also made it possible to allow angling for, e.g., the smallest type of mature salmon; that is, salmon less than 3 kg, or the so called 1SW, while all older (bigger) salmon must be released.¹ This new potential flexibility in management has however not yet been put fully into effect, and the difference in management practice between rivers is large. This may possibly hinge on the lack of analysis of what the best harvest regime would look like under different sea lice threats. The overall aim of this paper is hence to assess the economic loss of sea lice under different scenarios, and to explore to what extent the optimal harvesting policy is affected by sea lice-induced mortality.

Both 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

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.

based on age/stage structured biological models instead of the simplified biomass models. Due to the complexity of age structured models, economic studies based on such models have basically been case studies illustrated by numerical analysis. One noteworthy exception is Tahvonen (2009), who demonstrates analytical results on optimal harvesting under certain simplifying assumptions within a dynamic framework. See also Skonhøft et al. (2012), who analyzed a static maximum economic yield fishery with three age classes under perfect and imperfect selectivity, and demonstrated several analytical results that contrast what are found in the biomass models. Increased sea lice densities may be considered a type of biological pollution and thus a unidirectional externality running from the farmed salmon sector to the wild salmon sector. In a biomass framework McConnell and Strand (1979) analyzed the social returns to commercial fisheries when water quality influenced both demand and supply of commercial fish products under open access and when fish stocks were efficiently allocated. In closer relation to the present study, Massey et al. (2006) developed a stage structured bioeconomic model of the recreational Atlantic coast summer flounder fishery. They look at the benefits of improving the water quality conditions in Maryland's coastal bays. When the benefits are compared with estimates from a non-structural model, they find that the unstructured model is likely to lead to inaccurate predictions.

This study is structured as follows. The next section presents the age structured population model for wild salmon. In section three, costs and benefits are added, while the various management strategies are analyzed in section four. Next, in section five, the analytical results are evaluated by applying Norwegian salmon data in a numerical representation of the model. Some concluding remarks and management implications are given in section six.

2. Population model

Atlantic salmon is an anadromous species with a complex life cycle that includes several distinct phases. Freshwater habitat is essential for the early development stages, where it spends the first 1-4 years from spawning to juvenile rearing, before undergoing smoltification and seaward migration. It then stays from 1 - 3 years feeding and growing in the ocean, and, 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). The

Atlantic salmon is subject to fishing when it migrates back to its parent river. In Norway, sea fishing takes place in fjords and inlets with wedge-shaped seine and bend nets, and is commercial or semi commercial. In the rivers, salmon are caught by recreational anglers with fishing rods. The recreational fishery is the far most important from an economic point of view (NOU 1999), but in number and biomass of fish caught, these two fisheries are today more or less equivalent (Anon. 2011; Liu et al. 2011).²

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 has higher fertility than the young spawning salmon (McGinnity et al. 2003). Natural mortality is fixed and density independent, and as an approximation it is assumed that the whole spawning population dies after spawning. It is further assumed that the proportion between the three mature age classes is fixed. This proportion may be influenced by a number of factors, such as type of river ('small salmon river' vs. 'large salmon river') and various environmental factors (NOU 1999). As fishing takes place when the fish returns back to its 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 is found in e.g., Verspoor et al. (2003).

Figure 1 about here

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

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

² Note however, that more than half of the present commercial catch is caught in the Finnmark County, while in the remaining 18 counties, the commercial harvest is already shut down or rapidly decreasing due to strict regulations (see also below) Statistics Norway 2011.

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

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

where s_a is the age-specific natural survival rate, assumed to be density independent and fixed over time. Finally, we have the mature age classes that are subject to fishing mortality (marine as well as river fishing), 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:

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

where $0 \leq f_{4,t} \leq 1$ is the fishing mortality. $H_{4,t} = s_3 N_{3,t} \sigma f_{4,t}$ is accordingly the number of harvested 1SW mature fish at year t . As indicated, the parameter σ may vary due to, say, river type, but is considered as fixed and exogenous.

The rest of this cohort $s_3 N_{3,t} (1 - \sigma)$ stays one more year in the ocean. The proportion of the mature stock that returns to spawn after the second year is $0 \leq \varphi \leq 1$, and 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 this next year (2SW) spawning population becomes:

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

$0 \leq f_{5,t} \leq 1$ is the fishing mortality and $s_3 N_{3,t} (1 - \sigma) \varphi s_4 f_{5,t+1}$ is the number of harvested 2SW of this cohort year $t + 1$. The rest of this cohort $s_3 N_{3,t} (1 - \sigma - \varphi + \varphi \sigma) s_4$ stays one more year in the ocean. After natural mortality and subsequent fishing, the size of the next (third) year (3SW) spawning stock is:

$$(5) \quad N_{6,t+3} = s_3 N_{3,t} (1 - \sigma - \varphi + \varphi \sigma) s_4 s_5 (1 - f_{6,t+2}).$$

$0 \leq f_{6,t} \leq 1$ is the fishing mortality and $s_3 N_{3,t} (1 - \sigma - \varphi + \varphi \sigma) s_4 s_5 f_{6,t+2}$ is the number of harvested 3SW of this cohort year $t + 2$, with γ_4, γ_5 , and γ_6 as the fecundity parameters of the small (1SW), middle (2SW), and large (3SW) mature population, respectively. Note that these fecundity parameters are adjusted to take into account that there are different ratios of females and males at the different stages. The reason why there are different shares of females in the

1SW, 2SW, and 3SW stock, respectively, is 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 share of females at each stage is included (see also numerical section below).³ The spawning population year t may be written as

$$B_t = \gamma_4 N_{4,t} + \gamma_5 N_{5,t} + \gamma_6 N_{6,t}, \text{ or as:}$$

(6)

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

The fecundity parameters will be considered as dimensionless parameters; that is, when scaling the fertility of the 1SW class to one, $\gamma_4 = 1$, the fertility of the 2SW and 3SW class, simply indicates that B_t is measured as a fertility weighted number of spawning salmons. Equations (1) and (2) imply $N_{3,t+3} = s_0 s_1 s_2 N_{0,t}$, or:

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

when also using equation (2) and where $s = s_0 s_1 s_2$ comprises previous years survival rates. $N_{3,t}$ will subsequently be referred to as the potentially harvestable population, or simply the harvestable population. For given fishing mortalities, equations (7) and (6) yield a system of two difference equations of degree seven in the two variables $N_{3,t}$ and B_t .

3. Cost and benefits

With w_6 , w_5 , and w_4 as the fixed weights (kg per fish) of the 3SW, 2SW, and 1SW mature population, respectively, and where $w_6 > w_5 > w_4$, the biomass harvested (in kg) in year t is defined by $Y_t = w_4 s_3 \sigma f_{4,t} N_{3,t} + w_5 s_3 (1 - \sigma) \varphi s_4 f_{5,t} N_{3,t-1} + w_6 s_3 (1 - \sigma - \varphi + \varphi \sigma) s_4 s_5 f_{6,t} N_{3,t-2}$.

³ The implicit assumption is that there will always be enough males at the spawning ground.

To find the value of this biomass, prices of the different year classes and costs have to be taken into account. As indicated, the Atlantic salmon is targeted both by commercial fishermen and sport anglers. The sport fishing takes place in the rivers with rods, while the commercial, or semi commercial, takes place in the fjords and inlets with wedge-sized seine and bend nets. p_i ($i = 4, 5, 6$) are the net market prices (NOK per kg) and are assumed to be independent of total harvest, but will generally be dependent on the age classes, i.e., weight of fish, especially for commercial fisheries. The net market price is much higher in the recreational fishery than in the commercial fishery because the benefit of recreational fishing is measured by the price of fishing permits, or licenses, while the benefit of commercial fishing is measured by the meat value (Olaussen 2007). Hence, since the anglers typically pay for a one-day fishing permit, and the average catch per fishing day is quite low (see below), the benefit per kg of salmon is much higher in the recreational than in the commercial fishery.

In the following, we assume all harvest takes place in the river. There are two main reasons for this. First, due to strict regulations of the marine salmon fishery since 2008, sea fishing seems to gradually be fading away, and is already non-existent in many fjords (Statistics Norway 2011). Second, we want to look at the most valuable harvest pattern, and it is well known that this involves zero marine harvest (see e.g. Olaussen 2007; Liu et al. 2011). Therefore, p_i are determined by the value of salmon in the recreational fishery, and we typically have $p_6 \geq p_5 \geq p_4$ (Olaussen and Liu 2011). Additionally, the costs of recreational fishing are small and negligible, thus

$$\pi_t = p_4 w_4 s_3 \sigma f_{4,t} N_{3,t} + p_5 w_5 s_3 (1 - \sigma) \varphi s_4 f_5 N_{3,t-1} + p_6 w_6 s_3 (1 - \sigma - \varphi + \varphi \sigma) s_4 s_5 f_{6,t} N_{3,t-2}$$

represents the yearly economic gross benefit, or profit, of our salmon fishery, which may approximate net benefit, or profits.⁴

4. 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 both 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

⁴ See also the Appendix, where a recreational fishery model is explicitly formulated.

(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. In the present exposition, we are only concerned with equilibrium fishing, or sustainable harvesting. The population equilibrium for fixed fishing mortalities is defined for $N_{3,t} = N_3$ and $B_t = B$ for all t such that:

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

and

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

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 either f_4 , f_5 , or f_6 , or all, are below one; that is, if depletion is to be prevented, not all mature classes can be fished totally down. Notice that this is a necessary but not sufficient condition. Figure 2 illustrates the internal, unique equilibrium when the recruitment function is of the Beverton-Holt type, i.e., $R(0) = 0$ and $\partial R / \partial B_t = R' > 0$ and $R'' < 0$ (see also numerical section five).

Figure 2 about here

In line with intuition, we find that higher fishing mortalities shift the spawning constraint (6') upwards and yield smaller equilibrium stocks. On the other hand, higher survival rates yield more fish, as the spawning constraint (6') shifts down (both through s_3 , s_4 , and s_5), and the recruitment constraint (7') shifts up (through s). For a larger fraction of the young mature stock – that is, a higher value of σ – we find more spawning fish as well as more harvestable fish if the mortality and female share corrected fertility parameter is higher for the 1SW mature stock than the 2SW stock, i.e., $\gamma_4(1 - f_4) > \gamma_5 s_4(1 - f_5)$. For equal targeted stocks, $f_4 = f_5$, this simplifies to $\gamma_4 / s_4 > \gamma_5$ which may be interpreted as if the young mature stock ‘biologically discounted’ fertility dominates the old mature stock fertility. The same reasoning also holds when we compare 1SW with 3SW, or 2SW with 3SW.

The maximum sustainable economic yield problem is described by finding fishing mortalities that maximize equilibrium profit π subject to the spawning constraint (6') and the recruitment constraint (7'). The Lagrangian of this problem is written as:

$$(8) \quad L = [p_4 w_4 s_3 \sigma f_4 + p_5 w_5 s_3 (1 - \sigma) \phi s_4 f_5 + p_6 w_6 s_3 (1 - \sigma - \phi + \phi \sigma) s_4 s_5 f_6] N_3 - \lambda [N_3 - sR(B)] - \mu \{ B - [\gamma_4 s_3 \sigma (1 - f_4) + \gamma_5 s_3 (1 - \sigma) \phi s_4 (1 - f_5) + \gamma_6 s_3 (1 - \sigma - \phi + \phi \sigma) s_4 s_5 (1 - f_6)] N_3 \},$$

where $\lambda > 0$ and $\mu > 0$ (both in NOK per fish) are the shadow prices of the *recruitment* and *spawning* constraints, respectively. Following the Kuhn-Tucker theorem, the first-order necessary conditions (assuming $N_3 > 0$ and $B > 0$) are:

$$(9) \quad \partial L / \partial f_4 = N_3 (p_4 w_4 - \mu \gamma_4) \begin{matrix} \geq \\ < \end{matrix} 0; \quad 0 \leq f_4 \leq 1,$$

$$(10) \quad \partial L / \partial f_5 = N_3 (p_5 w_5 - \mu \gamma_5) \begin{matrix} \geq \\ < \end{matrix} 0; \quad 0 \leq f_5 \leq 1,$$

$$(11) \quad \partial L / \partial f_6 = N_3 (p_6 w_6 - \mu \gamma_6) \begin{matrix} \geq \\ < \end{matrix} 0; \quad 0 \leq f_6 \leq 1,$$

$$(12) \quad \begin{aligned} \partial L / \partial N_3 &= p_4 w_4 s_3 \sigma f_4 + p_5 w_5 s_3 (1 - \sigma) \phi s_4 f_5 + p_6 w_6 s_3 (1 - \sigma - \phi + \phi \sigma) s_4 s_5 f_6 - \lambda \\ &+ \mu [\gamma_4 s_3 \sigma (1 - f_4) + \gamma_5 s_3 (1 - \sigma) \phi s_4 (1 - f_5) + \gamma_6 s_3 (1 - \sigma - \phi + \phi \sigma) s_4 s_5 (1 - f_6)] = 0, \end{aligned}$$

and

$$(13) \quad \partial L / \partial B = \lambda s R'(B) - \mu = 0.$$

Control condition (9) indicates that the fishing mortality of the 1SW population should take place up to the point where the value of the marginal harvest biomass gain is equal, below or above its marginal reproduction loss determined by the fecundity parameter and evaluated by the spawning constraint shadow price. Conditions (10) and (11) are analogous for the 2SW and 3SW populations, respectively. The stock condition (12) says that the harvestable population should be managed so that the recruitment constraint shadow price is equal to the total marginal harvest gain plus the total marginal spawning biomass gain, evaluated at its shadow price. Finally, equation (13) indicates that the recruitment growth, evaluated at its shadow price, should be equal to the spawning constraint shadow price.

From the control conditions (9), (10), and (11), it is observed that only the biomass-value/fecundity ratio $p_i w_i / \gamma_i$ ($i = 4, 5, 6$) steer the fishing mortality and the fishing composition, and hence no other factors play a *direct* role. This outcome differs from the papers of Reed (1980) and Skonhøft et al. (2012), that found that weight together with natural mortality directly determined the fishing composition. As already indicated, the reason for this discrepancy is the different biological characteristics of the fish stocks: while the mature fish dies after spawning in our salmon model, the fish (e.g., cod) survives and enter older age classes in these other models.

Generally, the Kuhn-Tucker first order conditions give us thirty different potential harvest patterns. For example, when we have $p_4 w_4 / \gamma_4 > p_6 w_6 / \gamma_6 > p_5 w_5 / \gamma_5$, which is in accordance with our Norwegian wild salmon data (see numerical section), there will be five potential harvest patterns given 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) $f_4 = 1, f_6 = 0, f_5 = 0$, v) $0 < f_4 < 1, f_6 = 0, f_5 = 0$.⁵ Clearly, the most aggressive harvest pattern is given by case i), where the whole 1SW and 3SW sub populations are harvested. Then, harvest pattern ii) is less aggressive, and so on, with harvest pattern v) giving the lowest harvesting pressure; that is, only harvest some proportion of the 1SW. This can easily be confirmed by looking at the slope of the spawning constraint (6') in Figure 2.

The optimal selective harvest pattern will be compared with the outcome when the fishing takes place in a uniform manner; that is, fishing mortality is similar among all population classes. For example, this will be the case if catch and release fishing is forbidden for ethical reasons, since the fishing gear is non-selective (see also Appendix). Our economic problem is then to maximize the sustainable economic yield subject to the biological constraints (6') and (7) and the restriction that the same fishing mortality is applied for all harvestable classes, i.e., $f_4 = f_5 = f_6$.

⁵ The twenty-five remaining possibilities are found by assuming $p_4 w_4 / \gamma_4 > p_5 w_5 / \gamma_5 > p_6 w_6 / \gamma_6$, $p_5 w_5 / \gamma_5 > p_6 w_6 / \gamma_6 > p_4 w_4 / \gamma_4$, $p_5 w_5 / \gamma_5 > p_4 w_4 / \gamma_4 > p_6 w_6 / \gamma_6$, $p_6 w_6 / \gamma_6 > p_5 w_5 / \gamma_5 > p_4 w_4 / \gamma_4$, and $p_6 w_6 / \gamma_6 > p_4 w_4 / \gamma_4 > p_5 w_5 / \gamma_5$.

The Lagrangian of this problem may be written as $L = [p_4 w_4 s_3 \sigma + p_5 w_5 s_3 (1 - \sigma) \varphi s_4 + p_6 w_6 s_3 (1 - \sigma - \varphi + \varphi \sigma) s_4 s_5] f N_3 - \lambda [N_3 - sR(B)] - \mu \{B - [\gamma_4 s_3 \sigma + \gamma_5 s_3 (1 - \sigma) \varphi s_4 + \gamma_6 s_3 (1 - \sigma - \varphi + \varphi \sigma) s_4 s_5] (1 - f) N_3\}$ when inserting for the uniform fishing pattern. The first order necessary conditions, again with $N_3 > 0$ and $B > 0$), reads:

$$(14) \quad \begin{aligned} \partial L / \partial f &= N_3 [p_4 w_4 \sigma + p_5 w_5 (1 - \sigma) \varphi s_4 + p_6 w_6 (1 - \sigma - \varphi + \varphi \sigma) s_4 s_5] \\ &- \mu [\gamma_4 \sigma + \gamma_5 (1 - \sigma) \varphi s_4 + \gamma_6 (1 - \sigma - \varphi + \varphi \sigma) s_4 s_5] N_3 = 0; \quad 0 < f < 1 \end{aligned}$$

and

$$(15) \quad \begin{aligned} \partial L / \partial N_3 &= [p_4 w_4 \sigma + p_5 w_5 (1 - \sigma) \varphi s_4 + p_6 w_6 (1 - \sigma - \varphi + \varphi \sigma) s_4 s_5] f - \lambda \\ &+ \mu [\gamma_4 \sigma + \gamma_5 (1 - \sigma) \varphi s_4 + \gamma_6 (1 - \sigma - \varphi + \varphi \sigma) s_4 s_5] (1 - f) = 0 \end{aligned}$$

together with equation (13). The control condition (14) must hold as equation as stock depletion (as well as zero fishing) can never be beneficial under this economic yield scenario with zero discount rent. With $N_3 > 0$, this equation may also be written as

$$[p_4 w_4 \sigma / s_4 + p_5 w_5 (1 - \sigma) \varphi + p_6 w_6 (1 - \sigma - \varphi + \varphi \sigma) s_5] = \mu [\gamma_4 \sigma / s_4 + \gamma_5 (1 - \sigma) \varphi + \gamma_6 (1 - \sigma - \varphi + \varphi \sigma) s_5]$$

after some small rearrangements.

Therefore, the optimal uniform fishing pattern may be characterized as a situation in which the ‘biological discounted’ marginal harvesting value (marginal gain) equalizes the ‘biological discounted’ fertility (marginal loss), evaluated by the spawning constraint shadow value. This equation also determines the optimal spawning constraint shadow price, μ . This uniform harvest pattern can never be more economically beneficial than the selective harvesting scheme, as one more constraint is included in the non-selective maximization problem. When combining equations (14) and (15) we find $\lambda = \mu [\gamma_4 \sigma + \gamma_5 (1 - \sigma) \varphi s_4 + \gamma_6 (1 - \sigma - \varphi + \varphi \sigma) s_4 s_5]$. Inserted into condition (13), the size of the spawning biomass is next described as $R'(B) = 1 / s [\gamma_4 \sigma + \gamma_5 (1 - \sigma) \varphi s_4 + \gamma_6 (1 - \sigma - \varphi + \varphi \sigma) s_4 s_5]$. Under uniform harvesting, the optimal spawning stock size B may hence be described by biological parameters alone.

In addition to the two above described optimizing regimes, we will also study a management regime in which the baseline optimal uniform harvest rate is kept fixed under different sea lice

induced mortality levels. This harvest regime may reflect a situation in which catch and release is not allowed and the manager keeps regulations unchanged due to either ignoring the smolt survival and/or because he holds the traditional view that very few spawning salmons are required to fully recruit the river (NOU 1999; Olausen 2007).

5. Numerical results

Data

The above theoretical reasoning 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 Sheperd recruitment function that includes three parameters. In our generic model we choose a simpler function, and apply the Beverton-Holt

function. This function may be specified as $R(B) = r \frac{B}{1 + B/K}$ with $r > 0$ as the intrinsic growth

rate, or maximum number of recruits per (fertility adjusted) spawning salmon, and $K > 0$ as the stock level for which density dependent mortality equals density independent mortality. The size of rK is scaling the system ('size of the river'), and is assumed to be 40.000 (# of recruits). The value of r indicates the 'quality' of the river, and we choose $r = 400$ (# of recruits per spawning salmon) (for a discussion of this see Skonhoft and Logstein (2003)). Hence, we have $K = 100$.

Table 1 shows these values as well as all the other baseline parameter values used in the numerical analysis. When normalizing the fertility parameter for the young to one, $\gamma_4 = 1$ (see section 2 above), and using the fertility-weight function of McGinnity et al. (2003) together with the female/male shares for the different mature stages from Hvidsten et al. (2004), we find $\gamma_5 = 7.89$ and $\gamma_6 = 11.60$ 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 than the 3SW, which again is higher than that of 2SW; that is, $w_4/\gamma_4 > w_6/\gamma_6 > w_5/\gamma_5$. Note that the reason why the weight and fecundity rates do not follow the pattern we would expect under a concave fecundity-weight relationship ($w_6/\gamma_6 > w_5/\gamma_5 > w_4/\gamma_4$) is because of the different male/female ratios of the

different stages.⁶ The survival parameters are based on NOU (1999). Finally, as already indicated, the fish prices (NOK per kg) are calculated from the recreational fishing permit prices. The assumption here is that the fishing permit price in a typical salmon river may be about NOK 300 per day.⁷ Based on average catch success, this permit price translates into a fish price of NOK 350 (NOK/kg).⁸ In the baseline we assume the same price per kg for the old, middle and young mature age classes.

Table 1 about here

Results

With weight–fertility variations as $pw_4/\gamma_4 > pw_6/\gamma_6 > pw_5/\gamma_5$, we find that the potential optimal fishing mortality possibilities under the assumption of perfect fishing selectivity are given by cases i) - v) as described in Section 4. In the baseline scenario, we find that case i) with $f_4 = f_6 = 1$ and $f_5 = 0.52$ yields the optimal fishing mortality pattern. See Table 2 (first column). The profit becomes 5,517 (1,000 NOK). The consequences of sea lice-induced mortality are also demonstrated in Table 2. It is not possible to give an accurate estimate regarding how much the smolt survival is reduced due to sea lice induced mortality on a national scale. The effect varies between fjords, and from river to river. However, the effect on the smolt survival at the national level is considered to be strong, defined as being in the range of 25% to 75% by Anon. (2011). To take this variation into account, we assess the consequences at different sea lice-induced mortality levels, with a 40% smolt survival reduction as our “best guess”. When the smolt mortality increases such that the survival rate s decreases, the fishing mortality for 2SW decreases while it is still optimal to keep $f_4 = f_6 = 1$ at the 40% smolt survival reduction

⁶ 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=0.187, 2SW=0.683, and 3SW=0.611 (Hvidsten et al. 2004), we hence have $\gamma_5 = 7.89$ and $\gamma_6 = 11.60$ when γ_4 is normalised to 1.

⁷ Mork (2011) uses NOK 400, while Olaussen and Skonhoft (2008) use NOK 200. However, the variation between different rivers is large and are found to vary from NOK 50 to NOK 200,000 (Liu et al. 2011). Based on the average permit price in the rivers Orkla, Gaula, Nidelva, and Stjoerdalselva for the 2011 season, NOK 300 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 3.3kg (Statistics Norway 2011). Hence, the average price per kg is $300\text{NOK}/(0.26*3,3\text{kg})=350\text{NOK}/\text{kg}$.

($s=0.03$). With this survival rate, the profit is reduced by about 47% to 2,932 (1,000 NOK). The same harvest pattern is kept even for a 60% reduction in the smolt survival ($s = 0.02$). In this case, the profit is reduced significantly and is now only 1,718 (1,000 NOK), that is, about one third of the profit in the baseline scenario. Note that under this case i), it is seen directly from the spawning constraint condition (6') in Figure 2 that the slope of the equilibrium spawning constraint increases with a higher fishing mortality of the 2SW such that the size of the spawning stock reduces accordingly. Therefore, while in the baseline situation we find $B = 494$ (number of fish) it becomes 275 when $s = 0.02$. With an 80% reduction in the baseline smolt survival rate and $s = 0.01$, we find that it is still optimal to harvest the whole 1SW stage population, while the harvest of the 3SW is reduced to $f_6 = 0.98$, and there is no harvest of 2SW fish. We then have the above described case iii). The same case is still present when the smolt survival is further reduced to $s = 0.005$. Note that the N_3 harvestable population decreases relatively more than the spawning stock for all reductions in the survival parameter since fishing mortality is reduced to compensate for the low natural mortality. As a result, the profitability is reduced even more; that is, the profit in this case is only about 3% ($170/5,517$) of that of the baseline situation.

It may seem surprising that even when the smolt survival is reduced by 90%, the harvest is still quite aggressive. The reason is that the recruitment function is very steep at low stock levels. The shape of the recruitment function is determined by the parameters r and K , and the slope is increasing in both these parameters. However, these results also seem quite robust within reasonable ranges of parameter values. For example, under the baseline sea lice mortality pressure, the change from harvest pattern i) (most aggressive) to ii) does not occur before either r or K is reduced by more than 75%.

Table 2 about here

Table 3 reports the outcomes when the stocks are harvested through a uniform harvest pattern as described by equations (13) – (15). The harvestable stock, spawning stock, and harvests of the 1SW and 3SW classes are all the time less than under the optimally selective harvest regime presented in Table 2. The optimal uniform fishing mortality is gradually reduced when the smolt survival decreases due to the sea lice-induced mortality. For 1SW salmon, the optimal uniform

harvest rate is always lower than under selective harvest (Table 2), where the optimal fishing mortalities for 1SW is kept to 1 at all smolt survival rates. For 3SW fish, the optimal uniform harvest rate becomes higher than under selective harvest only when the smolt survival is reduced by 90% ($s=0.005$). The harvest of 2SW, however, is always higher under uniform harvest than in the selective harvesting case due to higher fishing mortality. As expected, this more restricted harvesting pattern with two fewer control variables also necessarily results in reduced profitability, as discussed in Section 4. More specifically, our analysis shows that allowing for different harvest rates for different age classes increases the profitability in the range from 9% (baseline case with $s = 0.05$) to 68% (when $s = 0.005$) depending on the survival rate of smolt. At $s = 0.03$ the profit is increased by about 13% if selective harvest is put in place.

Table 3 about here

Table 4 presents the results when we keep the optimal baseline uniform harvest rates $f_4 = f_5 = f_6 = 0.80$ fixed under different sea lice-induced mortality rates. These calculations hence yield stock changes and the accompanying economic losses when the smolt mortality rate increases while there is at the same time no adjustment in the harvesting pattern. Compared to the regime in which the uniform harvest rate is chosen optimally (Table 3), the losses of keeping the harvest rate fixed are rather modest when the sea lice-induced mortality is not too strong. For example, at $s = 0.03$ the loss compared to the optimal uniform rate found in Table 2 is only about 3%. However, when the smolt survival rate is reduced by 80% or more ($s \leq 0.01$), this fixed harvest rate regime leads to population extinction and hence all the harvesting benefit disappears. It is also interesting to note that harvesting all of the mature 1SW and 3SW salmon results in a dramatically greater conservation of stock than harvesting a similar fixed fraction of all the three mature stages, i.e., $f_4 = f_5 = f_6 = 0.80$ ($s = 0.01$, Tables 2 and 4). Our analysis shows that, compared to a fixed uniform harvest rate, allowing for different harvest rates for different age classes increases the profitability in the range from 9% (baseline case with $s = 0.05$) to 100% (when $s \leq 0.01$) depending on the survival rate of smolt (Tables 2 and 4).

Table 4 about here

We have already discussed sensitivity with respect to the biological parameters r and K . Sensitivity analyses suggest that the results are quite robust to other parameter changes as well. For example, a uniform price increase for all stages does not alter the harvest pattern since the relative value/fecundity ratio remains identical. On the other hand, if we allow for different prices at different stages, the harvest pattern may of course be altered according to the 30 different harvest compositions revealed in Section 4. For example, if the price of 2SW salmon (p_5) increases from the baseline NOK 350 per kg value to NOK 450, we find the optimal fishing described by case i) from Section 4. However, the main picture remains that, if we do not move too far away from the baseline values, the harvest pattern remains unchanged. This follows directly from the fact that the $p_4 w_4 / \gamma_4 > p_6 w_6 / \gamma_6 > p_5 w_5 / \gamma_5$ relationship is maintained within a wide range for relatively significant parameter changes.

6. Concluding remarks

In this paper, we have analyzed one example of the more general class of problems where man-made activities or actions provide challenges for various species. The overall aim of this paper has been to analyze how the harvest regimes and profitability of wild Atlantic salmon may be changed when external factors, such as increased sea lice density, reduces the natural smolt survival rate. If we look at the common management regime in Norwegian rivers in recent years, the typical management scheme has been to allow for some harvest of the smallest (1SW) salmon, and severely restrict the fishing of medium sized (2SW) and large (3SW) salmon. To harvest the oldest mature classes is typically also completely restricted in many rivers. In contrast to the present harvest regime in Norwegian salmon rivers, our study shows that it is always optimal to harvest the whole 1SW subpopulation. This is because 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, and because the other two stages are sufficient to secure recruitment in the river. Furthermore, since the biomass-value/fecundity relationship is higher for the 3SW than the 2SW, we find that all the 3SW should be harvested for all smolt survival rates except the two lowest (80% and 90% reduction). In these cases, the smolt survival is so low that also saving some of the 3SW is needed to secure sufficient recruitment. Not

allowing different harvest rates for different stages of the salmon stock turns out to reduce the profitability considerably, and seems to be more important the higher the sea lice density is. Moreover, to not adjust the uniform harvest rate according to the sea lice mortality may even lead to population extinction.

We have found that increased sea lice density does not necessarily call for altered harvest regimes, particularly when the mortality rates from sea lice infection was not too strong. In fact, we find surprisingly aggressive harvest patterns to be persistent even under quite high sea lice induced mortality situations. However, if a fixed uniform fishing mortality is applied, high sea lice induced mortality may drive the population to extinction. Thus, an optimal selective harvesting regime should be employed to secure both the highest potential profits and a viable population. Nevertheless, the increased sea lice density has profoundly reduced the harvestable stock, spawning stock and harvests of all age classes of salmon. Hence, even under a selective harvest pattern we have calculated economic losses to be up to 97%. On average, it seems likely that profits are reduced by nearly 50% due to increased sea lice induced mortality at the national level. We have also shown that, compared to an optimal uniform harvest rate, the economic losses due to sea lice mortality is reduced in the range of 9% to 67% if a selective harvest pattern is implemented.

In sum, there are some interesting points raised by the present analysis. First, allowing for different harvest rates for different age classes increases the profitability significantly. Second, choosing a fixed uniform harvest rate may lead to population extinction when the sea lice density increases rapidly. Finally, sea lice-induced mortality does not alter the harvesting patterns when sea lice infection is modest, but may still reduce profitability considerably.

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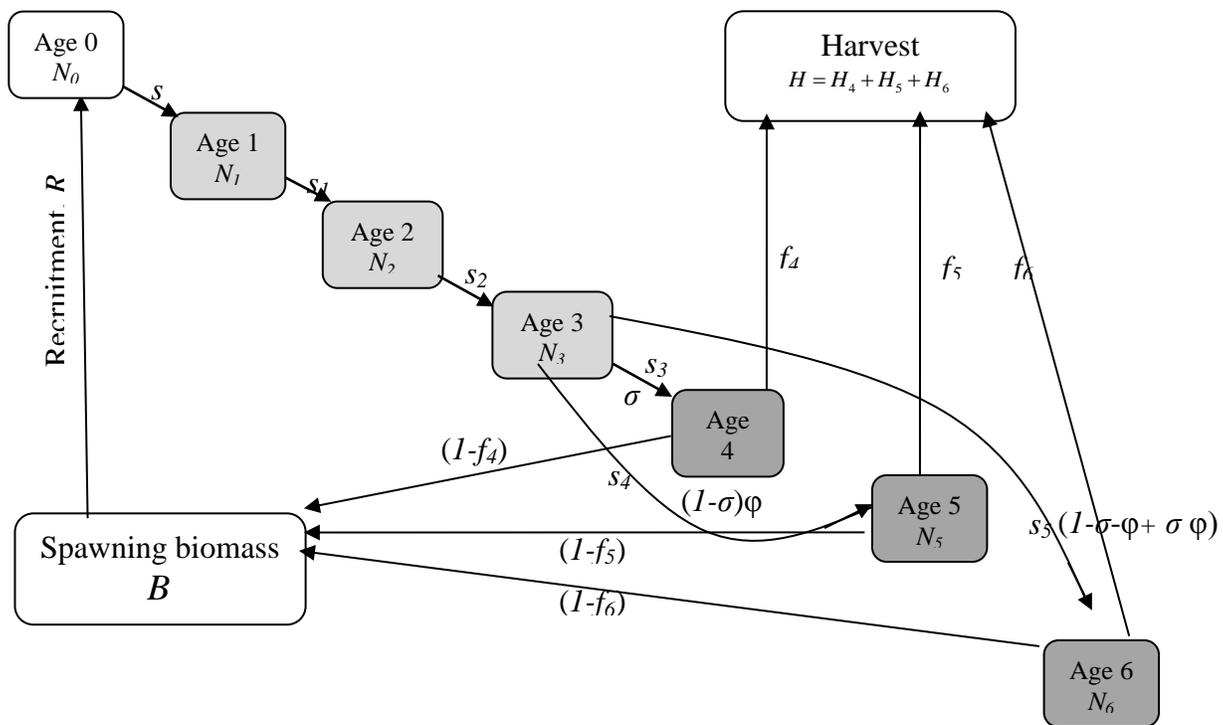


Figure 1. Schematic representation of the life cycle of a wild Atlantic salmon for a single cohort (the time index is omitted). See main text for definition of symbols.

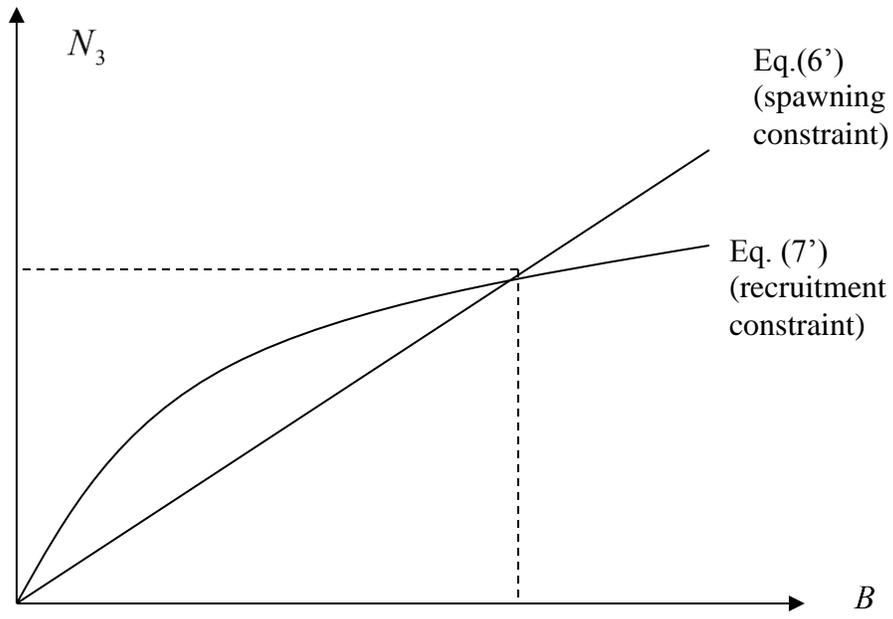


Figure 2. Internal equilibrium for fixed fishing mortalities $0 \leq f_4 \leq 1$, $0 \leq f_5 \leq 1$, and $0 \leq f_6 \leq 1$ (but not $f_4 = f_5 = f_6 = 1$). Beverton-Holt type recruitment function.

Table 1. Biological and economic baseline parameter values

| Parameter | Description | Value |
|------------|--|---|
| s | Natural survival rate young | 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) |
| 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 | 1.0 |
| γ_5 | Fecundity parameter 2SW | 7.9 |
| γ_6 | Fecundity parameter 3SW | 11.6 |
| p_4 | Fish price 1SW | 350 (NOK/ kg) |
| p_5 | Fish price 2SW | 350 (NOK/kg) |
| p_6 | Fish price 3SW | 350 (NOK/kg) |

Table 2: Optimal fishing mortalities under different sea lice-induced mortality levels

| | f_4 | f_5 | f_6 | N_3 | B | H_4 | H_5 | H_6 | π |
|----------|-------|-------|-------|-------|-----|-------|-------|-------|--------|
| Baseline | 1 | 0.52 | 1 | 1,663 | 494 | 358 | 68 | 53 | 5,517 |
| s=0.04 | 1 | 0.46 | 1 | 1,299 | 431 | 279 | 47 | 41 | 4,206 |
| s=0.03 | 1 | 0.38 | 1 | 933 | 359 | 202 | 28 | 30 | 2,932 |
| s=0.02 | 1 | 0.24 | 1 | 587 | 275 | 126 | 11 | 19 | 1,718 |
| s=0.01 | 1 | 0 | 0.98 | 240 | 151 | 52 | 0 | 8 | 617 |
| s=0.005 | 1 | 0 | 0.30 | 90 | 79 | 19 | 0 | 1 | 170 |
| s=0.1 | 1 | 0.66 | 1 | 3,524 | 740 | 758 | 182 | 113 | 12,380 |

Note: f_4, f_5 and f_6 are harvest rates for the 1SW, 2SW and 3SW class, respectively. N_3 is the potentially harvestable population while B is the spawning population. H_4, H_5 , and H_6 are the harvest (in number of salmon) of the 1SW, 2SW, and 3SW, respectively, while π is the yearly profit in 1,000 NOK. s is the lumped survival rate from the juvenile to the smolt stage.

Table 3: Optimal uniform fishing mortality under different sea lice-induced mortality levels

| | f_4 | f_5 | f_6 | N_3 | B | H_4 | H_5 | H_6 | π |
|----------|-------|-------|-------|-------|-----|-------|-------|-------|--------|
| Baseline | 0.80 | 0.80 | 0.80 | 1,593 | 391 | 273 | 99 | 41 | 5,058 |
| s=0.04 | 0.77 | 0.77 | 0.77 | 1,236 | 339 | 205 | 75 | 31 | 3,806 |
| s=0.03 | 0.74 | 0.74 | 0.74 | 884 | 280 | 140 | 51 | 21 | 2,600 |
| s=0.02 | 0.68 | 0.68 | 0.68 | 542 | 210 | 79 | 29 | 12 | 1,467 |
| s=0.01 | 0.54 | 0.54 | 0.54 | 218 | 120 | 26 | 9 | 4 | 474 |
| s=0.005 | 0.36 | 0.36 | 0.36 | 71 | 55 | 10 | 28 | 17 | 101 |
| s=0.1 | 0.86 | 0.86 | 0.86 | 3,424 | 594 | 630 | 229 | 94 | 11,690 |

Note: f_4, f_5 and f_6 are harvest rates for the 1SW, 2SW and 3SW class, respectively. N_3 is the potentially harvestable population while B is the spawning population. H_4, H_5 , and H_6 are the harvest (in number of salmon) of the 1SW, 2SW, and 3SW respectively while π is the yearly profit in 1,000 NOK. s is the lumped survival rate from the juvenile to the smolt stage.

Table 4: Fixed uniform fishing mortality under different sea lice-induced mortality levels

| | f_4 | f_5 | f_6 | N_3 | B | H_4 | H_5 | H_6 | π |
|----------|-------|-------|-------|-------|-----|-------|-------|-------|--------|
| Baseline | 0.80 | 0.80 | 0.80 | 1,593 | 391 | 273 | 99 | 41 | 5,058 |
| s=0.04 | 0.80 | 0.80 | 0.80 | 1,193 | 294 | 204 | 74 | 30 | 3,788 |
| s=0.03 | 0.80 | 0.80 | 0.80 | 793 | 195 | 136 | 50 | 20 | 2,520 |
| s=0.02 | 0.80 | 0.80 | 0.80 | 393 | 97 | 67 | 25 | 10 | 1,249 |
| s=0.01 | 0.80 | 0.80 | 0.80 | 0 | 0 | 0 | 0 | 0 | 0 |
| s=0.005 | 0.80 | 0.80 | 0.80 | 0 | 0 | 0 | 0 | 0 | 0 |
| s=0.1 | 0.80 | 0.80 | 0.80 | 3,593 | 884 | 615 | 224 | 92 | 11,410 |

Note: f_4, f_5 and f_6 are harvest rates for the 1SW, 2SW and 3SW class, respectively. N_3 is the potentially harvestable population while B is the spawning population. H_4, H_5 , and H_6 are the harvest (in number of salmon) of the 1SW, 2SW, and 3SW respectively, while π is the yearly profit in 1,000 NOK. s is the lumped survival rate from the juvenile to the smolt stage.

Appendix

Another reason for analyzing a uniform harvest pattern is that, under certain conditions, the results coincide with the results from models in which the recreational fisheries are studied under the assumptions of classical Schaefer harvesting technology and non-selective fishing gear. By introducing an inverse demand function for fishing permits, e.g. expressed in daily permits, and where the demand depends on the permit price z and the fish abundance N_3 , indicating the quality of the river (Anderson 1983, 1994; Olaussen & Skonhøft 2008), we may write the demand function as $z=z(D, N_3)$, with $\partial z / \partial D = z^D < 0$ and $\partial z / \partial N_3 = z^{N_3} > 0$. Further, when the cost function $c(D)$ of organizing the river fishery is assumed to have $c' > 0$ and $c'' < 0$, the current benefit is described by $\pi = z(D, N_3)D - c(D)$. Under Schaefer fishing technology, and where the number of fishing permits (days) represents effort, the catch functions for the 1SW, 2SW, and 3SW fish is written $H_4 = q_4 D N_3 s_3 \sigma$, $H_5 = q_5 (D \alpha_3 \varphi N$, and $H_6 = q_6 D N_3 s_3 (1 - \sigma - \varphi + \varphi \sigma) s_4 s_5$, respectively, and the fishing mortalities are hence defined by

$0 \leq q_4 D = f_4 \leq 1$, $0 \leq q_5 D = f_5 \leq 1$, and $0 \leq q_6 D = f_6 \leq 1$. Hence, with identical catchability coefficient, the fishing pattern is uniform. Moreover, with different catchability coefficients for 1SW, 2SW, and 3SW fish, the fishing mortalities will be governed by fixed ratios. The Lagrangian of maximizing $\pi = z(D, N_3)D - c(D)$ is now written as

$$L = z(D, N_3)D - c(D) - \lambda[N_3 - sR(B)]$$

$$- \mu \{ B - [\gamma_4 s_3 \sigma (1 - q_4 D) + \gamma_5 s_3 (1 - \sigma) \varphi s_4 (1 - q_5 D) + \gamma_6 s_3 (1 - \sigma - \varphi + \varphi \sigma) s_4 s_5 (1 - q_6 D)] N_3 \}$$

$-\eta(q_4 D - 1) - \psi(q_5 D - 1) - \varphi(q_6 D - 1)$ where η , ψ and φ are the shadow price for the 1SW fishing mortality constraint, the 2SW fishing mortality constraint, and the 3SW fishing mortality constraint, respectively. Now it is easily seen that as long as $q_4 = q_5 = q_6$, maximizing the overall (social) surplus of this problem yields the same structure in the optimality conditions as under the uniform harvest regime discussed above, only with number of permits as the control variable instead of fishing mortality. Hence, the structure of the results is the same, and with similar demand and supply conditions, the results coincide.