Interactions between grey seal (*Halichoerus grypus*), Atlantic salmon (*Salmo salar*), and harvest controls on the salmon fishery in the Gulf of Bothnia

P. Jounela, P. Suuronen, R. B. Millar, and M-L. Koljonen


Interactions between grey seal, Atlantic salmon, and harvest controls on the salmon fishery in the Gulf of Bothnia, northern Baltic Sea, were investigated for the period 1999—2003. We assessed the effects of seal-induced catch losses (fish damaged or eaten by seals in the fishing gears) and harvest restrictions (delayed sequential opening of the fishery from south to north) on the Finnish coastal salmon catch and on escapement of salmon into the Tornionjoki River, the major breeding ground of the species in the Baltic Sea. Commercial logbook data on catches and seal-induced catch losses were used in a stochastic Monte Carlo analysis, indicating that mainly because of the stricter harvest controls enforced in 1996 and 1997, the average annual spawning run abundance that approached the Finnish coastal area increased by ca. 56 700 fish between 2000 and 2002. However, these fish were caught increasingly in the northern Gulf of Bothnia (Management Areas, MAs, 3 and 4), and relatively few salmon escaped into the Tornionjoki River. The landings in MAs 3 and 4 increased by 57% and 144%, respectively, whereas in the southern Gulf of Bothnia (MA 1), landings decreased by 23%. Over the five years of the study, seal-induced catch losses in MA 1 ranged from 24% to 29% of the total catch, whereas in MAs 2, 3, and 4 it ranged from 3% to 16%. The analysis suggests, however, that in MA 1 the regulation-induced catch losses were even higher than seal-induced catch losses, indicating that the salmon fishery was being impacted by both major factors. To increase escapement into the river and potentially to increase the future wild salmon catch, the opening of the harvest in the northernmost MAs should be delayed. Seal-induced catch losses should be reduced by extensive introduction of seal-safe fishing gears and by sustainable control of the grey seal population.

Keywords: *Halichoerus grypus*, harvest restrictions, *Salmo salar*, seal-induced catch losses, seal—salmon fishery interactions, spawning escapement.

Introduction

The construction of hydroelectric power plants and other anthropogenic activities significantly reduced or totally eliminated the natural reproduction of wild Atlantic salmon (*Salmo salar*) stocks in most Baltic salmon rivers (Christensen *et al*., 1994; Karlsson and Karlström, 1994). To compensate for the effects of shrinking wild salmon stocks, extensive salmon stocking programmes were launched in the 1960s and 1970s in Finland and Sweden. These stocking programmes supported the growth of a major offshore salmon fishery in the Baltic Proper and in the Gulf of Bothnia. However, the offshore fishery was a mixed stock fishery of wild and hatchery fish, and it therefore also increased the fishing pressure on the shrinking wild stocks (Jutila, 1992; Pruuki, 1993; Karlsson and Karlström, 1994; Karlström, 1995). By the end of the 1980s, several wild stocks in the northern Baltic Sea were either extinct

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or close to extinction (Kaukoranta et al., 2000; Romakkaniemi et al., 2003).

Various types of management initiatives were enforced in the 1970s and 1980s in the Baltic salmon fishery to reduce fishing effort (Christensen et al., 1994). Total allowable catches (TACs) were introduced in 1991. Partly due to stricter fishing regulations, the offshore fishery declined considerably in the early 1990s, and in the Gulf of Bothnia, the offshore fishery for salmon practically ceased in the late 1990s. Subsequently, most of the salmon catch in the Gulf of Bothnia was harvested by large floating trapnets (see Kauppinen et al., 2005) moored near the coast along the migration routes of salmon. These management actions, however, did not markedly increase the abundance of wild salmon stocks. In 1996, delayed sequential openings were introduced in the Gulf of Bothnia salmon fishery to increase escapement of wild stocks. The Finnish side of the Gulf of Bothnia was divided into four Management Areas (later referred to as MAs 1–4; Figure 1), and the opening day of the fishery was delayed until 21 June in MA 1, and sequentially delayed by an additional five days in each of MAs 2, 3, and 4. These restrictions reduced total salmon catches and thereby markedly improved the escapement of wild salmon into the major salmon rivers in the northernmost part of the Gulf of Bothnia (Romakkaniemi et al., 2003). From 1998 to 2004, the opening days of the coastal fishery were brought forward by opening five days earlier in all four MAs, beginning on 16 June in MA 1.

In concert with the stricter harvest regulations, the rapidly growing grey seal (Halichoerus grypus) population (Halkka et al., 2005; Stenman et al., 2005) caused further catch losses to the commercial fishery by eating and damaging substantial numbers of the salmon caught in the trapnets (Kreivi et al., 2002; Kauppinen et al., 2005). The ringed seal (Phoca hispida bottnica) also caused damage in the northern Gulf of Bothnia, but substantially less than the grey seal (Westerberg et al., 2000; Kauppinen et al., 2005). The negative impact of seals on salmon fisheries varied considerably, from being barely discernible to involving a complete loss of catch and permanent damage to the fishing gear (Kauppinen et al., 2005). In particular, in the southern Gulf of Bothnia, extensive seal-induced catch losses together with strict harvest regulations have dramatically reduced the income of fishers. This situation has been very difficult for many fishers to understand and to accept, because wild salmon stocks have been growing while their fishing opportunities and catches have been decreasing.

To properly manage the salmon fishery and seals, and to reduce the likelihood of potential conflicts, it has become increasingly crucial to understand the temporal and spatial relationship between seal and regulation-induced factors on salmon stocks and the fishery. Previous works examined the effects of seal-induced catch losses (Kreivi et al., 2002; Kauppinen et al., 2005) and management measures (Romakkaniemi et al., 2003) on the salmon fishery. However, they did not quantitatively analyse the combined effects of these factors and the interactions between them.

The objectives of this study are to demonstrate the effects and potential interactions of (i) timing of the spawning migration, (ii) coastal harvest restrictions (delayed opening), (iii) abundance of salmon approaching the Finnish coastal area, and (iv) seal-induced catch losses on coastal salmon catches and escapements into the Tornionjoki River. This salmon stock was chosen as an indicator because it is, along with the Kalix stock, the major wild salmon stock in the Baltic Sea in terms of production potential (Anon., 2004). The main goal is to find feasible solutions to overcome or at least to mitigate the problems caused by the burgeoning seal population and strict harvest controls. These solutions should be fair to fishers but also effectively promote sustainable utilization of growing wild salmon stocks along the Finnish coast now and in future.

Material and methods

Data

ICES catch data (Anon., 2003, 2004) were used to estimate survival rates of salmon in each MA (Figure 1). The commercial catch data from the marine areas are based on fishery logbooks, and the river data are estimates of

Figure 1. The four management areas (MAs 1–4) along the spawning migration routes of salmon in the northern Baltic Sea and the Gulf of Bothnia. The main feeding area of salmon is in the southern Baltic Sea. The main wild salmon rivers flow into Bothnian Bay, the northernmost part of the Gulf of Bothnia.
catch based on enquiries that have been conducted among recreational fishers who bought fishing licenses. The Tornionjoki River catch data (Anon., 2004) were transformed from kilogrammes to numbers of fish using the mean weights of salmon published in the most recent annual catch report (Haikonen et al., 2005). Seal-induced catch-loss information for the Finnish coastal area has been collected since 1999 in fisheries logbooks, and is based on observations by fishers of damaged fish in their fishing gear when they haul it in (usually daily). The data used in this study consist of the number of salmon damaged (or partly eaten) by seals by gear by date by ICES rectangle, from 1999 to 2003. The catch-loss data do not contain information on seal species, but on the basis of earlier studies we assume that most losses are caused by grey seals (Kauppinen et al., 2005). Catch loss reported by trapnet fishers in their logbooks is similar to the estimates of catch loss (%) made by observers of the Finnish Game and Fisheries Institute, FGFRI (Kreivi et al., 2002; Kauppinen et al., 2005). Hence, the commercial catch-loss data can be considered reasonably reliable for this analysis. Note that the ratio of damaged to total catch will still be reliable even if the actual numbers are misreported.

Structure of the model

The timing of the spawning migration was calculated using catch rate (cpue) data from the entire migratory period. Then, using the relative harvest rate of salmon in the four MAs, we constructed a model to simulate the effect of different opening dates. This simulation randomizes over a range of uncertainties in model inputs, including the number of fish in the spawning migration, uncertainty in estimating the timing of the spawning migration, and the relative proportion entering the Tornionjoki River.

The simulation approximates the migrating population according to the possible outcomes for each fish. These include the fish being caught and landed at sea, being caught and damaged by seals, and being a survivor from the coastal fishery. In addition, of those fish that reach the rivers, we determine the contribution resulting from protection by the coastal harvest regulations.

Fish migration in respect to date and latitude

The temporal and spatial accumulation of daily catch rates from approximately 300 commercial trapnets along the Finnish coast for the period 1981–1985 (i.e. before the introduction of delayed opening harvesting control measures) was considered to correspond to the timing of the spawning migration (FGFRI, unpublished data). This is a reasonable assumption, because fishing effort remains relatively constant throughout the entire season. Therefore, the catch at any given location and time is proportional to the density of fish that would be present in the absence of fishing. In addition, we used trapnet catch accumulation data from a tagging study conducted in 2002 during the entire spawning migration of salmon (FGFRI, unpublished data). Latitude was used as an explanatory factor because the spawning migration starts from feeding areas in the southern Baltic Sea (Main Basin) and ends in the northern spawning rivers flowing mainly into Bothnian Bay (Figure 1). Within each of 30 latitudinal groups, the catch accumulation (i.e. total catch-to-date) was divided by the total catch for the season in that latitudinal group, giving an estimate of the proportion-to-date of the spawning migration having reached that latitude. These proportion-to-date estimates were modelled using a logistic curve of the form

\[ P_{\text{lat},d} = \frac{\exp(\alpha + \beta \times \text{lat} + \gamma \times d)}{1 + \exp(\alpha + \beta \times \text{lat} + \gamma \times d)} \]

where \(\alpha\), \(\beta\), and \(\gamma\) are parameters to be estimated, \(\text{lat}\) = latitude, and \(d\) = Julian day. Non-linear least-squares regression analysis (Rem NONLIN; SYSTAT, 2002) was used to estimate \(\alpha\), \(\beta\), and \(\gamma\).

In each of the four MAs, most fishing effort is in the northermost latitudes, so we define the proportion-to-date in the \(i\)(th) MA by \(P_{i,d}\), given by

\[ P_{i,d} = \frac{\text{the reported catch (from the ICES data) in the } i\text{-th MA by } d}{\text{the total catch for the season in the } i\text{-th MA by } d}, \]

where \(\text{lat}\) is the northermost latitude of MA \(i\), \(i = 1,...,4\).

Estimation of catch and escapement

In the survival estimation, it is assumed that fish that migrated through Finnish coastal waters before opening of the fishery were protected, whereas fish that migrated through after opening of the fishery were exposed to harvest. We modelled the predicted total annual catch (in numbers, and including seal-induced catch losses) of fish in each MA as a function of the opening date. For the \(i\)(th) MA \(i = 1, 2, 3,\) and 4), this total catch is a product of the spawning run abundance approaching MA 1 from the southern Baltic feeding grounds, \(N_1\), proportion of salmon yet to migrate through the MA at Julian date \(d\), \(1 - P_{i,d}\), and the proportion of salmon killed by fishing activity (caught, or taken by seals) in the MA during the legal fishing season. That is, the predicted total catch in each MA for a fishing season beginning on Julian date \(d\) is

\[ c_{i,d} = (1 - P_{i,d}) \times N_1 \times \left( \frac{C_i}{C_{\text{tot}} + C_R + s} \right) \]

\[ = (1 - P_{i,d}) \times N_1 \times \left( \frac{L_i + D_i}{L_{\text{tot}} + D_{\text{tot}} + C_R + s} \right), \quad i = 1, 2, 3, \text{ and } 4. \]

Here, \(C_i = L_i + D_i\) is the reported catch (from the ICES data) in the \(i\)(th) MA, and \(C_{\text{tot}}\) is the sum of the landed catch.
\( L_i \) and the number of seal-damaged fish \( D_c \). Similarly, the totals over the four MAs are denoted by \( C_{\text{tot}} = L_{\text{tot}} + D_{\text{tot}} \). The realized catch in all rivers is denoted by \( C_R \), and \( s \) is the estimated reference spawning stock size in other Bothnian Bay rivers (i.e. spawning stock size without the delayed harvest restrictions in Rivers Oulujoki, Iijoki, Simojoki, and Kemijoki). Without the delayed harvest restrictions, the reference spawning stock sizes in the other coastal Finnish rivers were assumed to total some tens or hundreds of fish only (Anon., 2004). Consequently, the value of \( s \) in Equation (3) has a negligible effect on the simulation results.

The number of fish escaping the marine commercial fishery is given by

\[
N_1 - \sum_{i=1}^{4} c_{i,d}.
\]  

A proportion, \( \delta \), of these enter the Tornionjoki River, so the number of fish entering the Tornionjoki River is

\[
N_{\text{TR}} = \delta \left( N_1 - \sum_{i=1}^{4} c_{i,d} \right).
\]  


The simulations and the estimation of annual total spawning run abundance, \( N_1 \), are explained in the Appendix. Figure 2 demonstrates how the estimated annual total spawning run abundance, \( N_1 \), is apportioned according to the annual stock proportion estimates. All survivors escape either into the Tornionjoki River or into the other rivers of Bothnian Bay.

**Results**

The estimated annual spawning run in the Finnish coastal area increased by 56 700 fish (+47%) from 2000 to 2002, then decreased by 10 700 fish (−6%) from 2002 to 2003 (Table 1, Figure 3). The bigger spawning run increased catches in MA 4 and the estimated escapements in the period 2001—2003 in the Tornionjoki River (Figures 4 and 5, Table 1). The estimated increase in the spawning run abundance during the years 2000—2003, however, did not result in an increase in the reported salmon catch in MA 1 and in the Tornionjoki River (Table 1, Figure 6). During the years 1999—2003, the landed catch in MA 1 decreased by 26%, whereas that in MA 2 remained approximately the same. The landed catches in MAs 3 and 4 increased by 57—144%.

In MA 1 the seal-induced catch loss ranged between 24% and 29% of the total catch, whereas in MAs 2—4 it was on average 3—16% (Table 1). During the period 2000—2002, the bigger spawning run increased the reported total coastal catches (including catch losses) by just 12 100 fish. In other words, the remaining fish (i.e. 56 700 – 12 100 = 44 600) either escaped into the rivers or were harvested and misreported, or both.

The parameter estimates of the spawning migration model are given in Table 2. The variation in the estimated timing of the spawning migration was 27 days (Figure 7). The estimated timing of the spawning migration in MA 3 was similar to that in MA 4, suggesting that there is no reason to separate these two MAs from each other. The analysis suggests that if the timing of the spawning migration is

![Figure 2](https://academic.oup.com/icesjms/article/63/5/936/664169/Downloaded)  

Figure 2. The survivors escape either into the Tornionjoki River, \( N_{\text{TR}} \), or into the other rivers, \( N_{\text{other rivers}} \), of Bothnian Bay. All survivors, \( N_{\text{All rivers}} (= N_{\text{TR}} + N_{\text{other rivers}}) \), are apportioned according to the annual stock proportion estimates. If the coastal salmon fishery is closed for the entire fishing season (i.e. the opening day of harvest is at day ~220 or later in MA 1), the total escapements in all Bothnian Bay rivers, \( N_{\text{All rivers}} \), equal \( N_1 \) in the southern Gulf of Bothnia.
exceptionally late and the delayed harvest restrictions are similar to those enforced in 1999–2003, 93–94% of the survivors from MAs 1 and 2 are exposed to harvest in MAs 3 and 4 (4000 iterations; Table 3). In an average timing of a spawning migration, 63–69% of fish are exposed to harvest in MAs 3 and 4. This is related only to those survivors that do not migrate along the coast through the so-called “terminal” fishing areas, where fish are exposed to legal harvest also during the closed period (terminal fishing areas are in the mouths, i.e. the estuaries, of the dammed rivers where the large compensatory stockings are made).

The results suggest that the timing of the spawning run was not exceptionally late in 1999 and 2001, because the reported river catches in the Tornionjoki River were greater than the minimum escapement estimates (Table 1). In 2000, all escapement estimates on the opening day of the fishery were less than the reported river catches, i.e. our estimates of escapement are possible outliers with respect to actual escapements.

**Discussion**

Our simulations suggest that an increase in escapement of salmon in the Tornionjoki River would be better secured if the delayed harvest control would be as it was in 1996.
Figure 4. The estimated landed salmon catch (black dots) in MAs 1–4 with different opening days (Julian day 167 = 16 June) of the coastal fishery of MA 1, and the estimated potential salmon catch (grey dots) when the seal-induced catch losses of salmon fall to zero. The reported landed catches for 1999–2003 are marked with large white circles. The reported landed catches + reported seal-induced catch losses of salmon are marked with large black circles. Note that some large circles are overlapping.

Figure 5. Estimated escapement based on the model (grey dots) with different opening days of the coastal fishery in MA 1. The large variations in the estimated escapements in 1999 and 2001 are a consequence of uncertain stock proportion estimates of Tornionjoki fish. The negligible escapement in 2000 is mainly due to a very small stock proportion estimate of Tornionjoki fish.
and 1997 (i.e. the opening date five days later than in the period 1999-2003). Romakkiemi et al. (2003) demonstrated that the strict control enforced in 1996 and 1997 clearly strengthened the salmon spawning stock sizes in the rivers of Bothnian Bay, although other factors were acting simultaneously. It is of note that the proportion of wild salmon in the commercial catches has increased since 1998 in all parts of the Baltic Sea (except in the Gulf of Finland); the share of wild salmon is now well over 50% in the Gulf of Bothnia, whereas a few years ago it was just 20-40% (Anon., 2004; Koljonen, in press). This increase is consistent with the fisheries restrictions launched in particular in 1996 and 1997 in the coastal fishery of the Gulf of Bothnia. In our simulations, the estimated spawning run abundance was highest in the years 2001-2003. This is consistent with the strict restrictions enforced in 1996 and 1997 (note that Baltic salmon usually stay the first three years of their life in the river, then on average 2-3 years at sea).

Without the strict fisheries restrictions enforced in 1996 and 1997 and the subsequent recovery of wild salmon stocks, the coastal salmon fishery would likely have experienced very low catches in the 2000s. This is because the post-smolt mortality of hatchery-reared salmon has

Table 2. Parameter estimates and correlation matrix of the spawning migration accumulation model in 1981-1985 + 2002 ($r^2 = 0.893$) and 2002 ($r^2 = 0.906$).

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Estimate</th>
<th>s.e.</th>
<th>Lower 95% CI</th>
<th>Upper 95% CI</th>
</tr>
</thead>
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<tr>
<td>1981-1985 + 2002</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Intercept ($\alpha$)</td>
<td>18.5785</td>
<td>1.5768</td>
<td>15.4879</td>
<td>21.6691</td>
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<td>Latitude ($\beta$)</td>
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<td>-0.4961</td>
</tr>
<tr>
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<td>0.0032</td>
<td>0.0871</td>
<td>0.0997</td>
</tr>
<tr>
<td>2002</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Intercept ($\alpha$)</td>
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<td>8.74622</td>
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<td>30.57745</td>
</tr>
<tr>
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<tr>
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<td>0.01131</td>
<td>0.05252</td>
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</table>

Correlation matrix

<table>
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<th>$\beta$</th>
<th>$\gamma$</th>
</tr>
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<tbody>
<tr>
<td>1981-1985 + 2002</td>
<td></td>
<td></td>
<td></td>
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<tr>
<td>Intercept ($\alpha$)</td>
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<td>0.3846</td>
</tr>
<tr>
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<tr>
<td>2002</td>
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<tr>
<td>Intercept ($\alpha$)</td>
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<tr>
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<td>-0.4169</td>
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<tr>
<td>Date ($\gamma$)</td>
<td>0.2234</td>
<td>-0.4169</td>
<td>1</td>
</tr>
</tbody>
</table>

Figure 6. The reported landed catch in 1980-2003 in MAs 1-4 and in the Tornionjoki River.
dramatically increased in the Baltic Sea since the early 1990s (Michielsens et al., 2006). Consequently, there have been less hatchery-originating adult salmon to support the coastal fishery. Clearly, the adequate escapement of wild salmon to the spawning rivers and the production of wild fish have become a lifeline to the coastal fishery. However, that lifeline has been of little comfort to many fishers, particularly those in the southern Gulf of Bothnia, given that grey seals have increasingly utilized the regulation-induced surplus by destroying catches. In some areas recently, the salmon fishery has been totally wiped out.

Our analysis suggests that in MA 1, the regulation-induced catch losses were even higher than the seal-induced catch losses, indicating that the salmon fishery in the area suffered considerably from both major factors. Moreover, our estimates of regulation-induced catch losses are too low if landed catches from the legal fishing season are under-reported. It appears most likely that many of the regulation-induced survivors were harvested in the Gulf of Bothnia and that these catches apparently were misreported in some area(s). That is because even a major increase in the estimated spawning run abundance did not increase catches in the Tornionjoki River. During the years 1999–2003, the river catches generally fell in the other Finnish coastal wild salmon rivers as well. If the regulation-induced survivors were caught in any coastal area during the prohibited fishing season (including the coastal “terminal areas”), the escapements in the Tornionjoki River were overestimated.

Further, the seal-induced catch losses reported in the logbooks may underestimate the actual number of salmon taken by seals from the gear. That is because many of the damaged or partly eaten fish may have been rinsed out of the gear without being recorded or seen, and seals may also have taken fish directly from trapnets (Lehtonen and Suuronen, 2004; Fjälling, 2005; Kauppinen et al., 2005.). If the magnitude of unnoticed and unreported seal-induced catch losses is notable during the legal fishing season, then we have underestimated the number of regulation-induced survivors. For the Swedish fishery, Fjälling (2005) estimated that the traditional method of assessing losses by counting the remains of fish underestimated losses by 46%. In the absence of studies on unnoticed seal-induced catch losses in Finland, we were unable to correct this potential underestimate in our assessment.

Growing seal populations have caused increasing problems to fisheries in many other areas along the coasts of the northeast Pacific and northern Atlantic (Spalding, 1964; Olesiuk et al., 1990a,b; Haug and Nilssen, 1995; Morris, 1996; Cairns et al., 2000; Moore, 2003). In British Columbia, Canada, the predation of out-migrating and returning fish by seals reduces the survival of depressed salmon stocks (Bigg et al., 1990; Olesiuk et al., 1995). The growth of the grey seal population will likely continue in the northern Baltic Sea, and seals may increasingly prey on salmon at sea and in the estuaries of wild salmon rivers. It would be useful therefore to assess the effect of natural predation by seals on the salmon stocks in the Baltic Sea.

Our results show that owing to strict harvest controls and seal attacks, there are extensive catch losses in particular in the southern Gulf of Bothnia. Clearly, to maintain a profitable salmon fishery in all management areas, catch losses should be drastically reduced. One possible way to do
this would be to open the harvest earlier, i.e. less strict harvest control in the southern Gulf of Bothnia. An earlier opening day would, however, reduce the escapement of wild salmon into spawning rivers, which would then result in lesser smolt production and a lower catch potential of salmon a few years later. The earlier opening would also mean an earlier start of seal-induced catch losses, i.e. seals would consume more salmon in total. A more sustainable management action to reduce catch losses would be an extensive adoption of seal-safe fishing gears. Seal-safe fishing gears (Lunney et al., 2003; Lehtonen and Suuronen, 2004) prevent seals from attacking the catches in the trapnets. However, they do not prevent all damage, and they may have a lesser capture efficiency and a higher price (Suuronen et al., in press).

Selected hunting of seals during the most active fishing season in the vicinity of fishing gears may reduce the total number of seals attacking the trapnets, but there is no scientific evidence that such action would reduce the losses. Moreover, such hunting may be difficult to conduct effectively and ethically. Sustainable control of the grey seal population, however, may be necessary if a profitable coastal fishery is going to be maintained along the Gulf of Bothnia.

In conclusion, our results indicate that the salmon fishery is experiencing marked seal-induced catch losses, and that these losses will likely increase in future if no mitigation measures are taken. To increase salmon escapement into the Tornionjoki River and to increase future wild salmon catch potential in all MAs, the opening days of harvest in the northernmost management areas should ideally be delayed.

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References


Appendix
Simulations

The parameter estimates of \( P_{\text{stat}} \) (Equation (1)) were exported into RISK (Industrial 4.5; Palisade Corporation, 2004) where we estimated \( P_{\text{stat}} \) for the northernmost latitude of MA i, \((i = 1, \ldots, 4)\) on Julian day \( d \), \((d = 110, \ldots, 210)\), and annual \( N_1 \), \( c_{\text{in}} \), and \( N_{\text{tr}} \) values (Equations (2–5)). The stochastic Monte Carlo (MC) simulations of \( P_{\text{stat}} \) included estimation uncertainty and statistical correlation of the migration timing curve parameters \( \alpha \), \( \beta \), and \( \gamma \). The estimate of \( P_{\text{stat}} \) used for 2002 was obtained using only the trapnet accumulation data from that year; for the other years (1999–2001 and 2003) we used the trapnet catch accumulation data from 1981 to 1985, and 2002.

The MC-simulations comprised two steps: first we estimated annual \( N_1 \) by using genetic algorithm (GA) optimization (Goldberg, 1989) with MC simulation (RISK Optimizer 1.0, www.palisade.com), then we simulated the interactions between seal, salmon, and harvest controls of the salmon fishery. In this second step, we used annual \( N_1 \) estimates obtained in the first step.

GA optimization with MC simulation

The annual spawning run abundance of salmon \((N_1)\) was estimated by minimizing the sum of squared error between the actual and predicted coastal catch and catch loss on the annual opening date of the fishery in each MA. GA optimization was used to attain the global minimum of the error surface. Generally, GA optimization is used when the objective function is highly non-linear, stochastic, or has unreliable or undefined derivatives. Here, the objective function (i.e. the least-squares solution) was non-linear and stochastic because of the logistic \( P_{\text{stat}} \) curve (Equation (1)), and hence MC simulation methods were applied.

When estimating annual \( N_1 \) by GA optimization, a set of (MC) simulations was generated for each possible trial least-squares solution. In each iteration of a trial solution’s simulation, probability distribution functions were sampled and changing \( N_1 \) generated a new value for the least-squares solution. At the end of a simulation, the result for the trial solution was the statistic for the distribution of the target cell, which was minimized. This value was then returned to the optimizer and used by it to generate new and better trial solutions. For each new trial solution, another simulation was run and another value for the target statistic was generated. Overall, we generated 100 simulations that contained 1000 iterations each to estimate the annual probability distribution of \( N_1 \). Before the GA optimization with MC simulation began, the minimum annual constraint of \( N_1 \) was set equal to annual sum of \( C_{\text{tot}} + C_R + s \) whereas the maximum constraint was set high, up to 250 000. Note that a change in the maximum constraint affects the standard deviation estimates of \( N_1 \), but not the median estimates of \( N_1 \), which were used in the final simulations of interactions between seal, salmon, and harvest controls of the salmon fishery.

Simulations of interactions

After solving the annual probability distribution of \( N_1 \) using GA optimization with MC simulation, we used annual median estimates of \( N_1 \) and \( \delta \) in the simulations of interactions between seals and harvest controls. That is because the estimated confidence intervals of \( N_1 \) and \( \delta \) were wide. In the results, however, we present separately each factor’s high uncertainties. The method of estimating wild Tornionjoki stock proportion is described in Koljonen et al. (2005), and the proportion of the wild stock group in Finnish Baltic salmon catches in Koljonen (2004, 2006).