A Bayesian state-space mark-recapture model to estimate exploitation rates in mixed stock fisheries

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Abstract

A Bayesian state-space mark-recapture model is developed to estimate the exploitation rates of fish stocks caught in mixed stock fisheries. Expert knowledge and published results on biological parameters, reporting rates of tags and other key parameters are incorporated into the mark-recapture analysis through elaborations in model structure and the use of informative prior probability distributions for model parameters. Information on related stocks is incorporated through the use of hierarchical structures and parameters that represent differences between the stock in question and related stocks. Fishing mortality rates are modelled using fishing effort data as covariates. A state-space formulation is adopted to account for uncertainties in system dynamics and the observation process. The methodology is applied to wild Atlantic salmon (*Salmo salar*) stocks from rivers located in the north-eastern Baltic Sea that are exploited by a sequence of mixed and single stock fisheries. Estimated fishing mortality rates for wild salmon are influenced by prior knowledge about tag reporting rates and salmon biology and to a limited extent by prior assumptions about exploitation rates.

Keywords: mark-recapture, mixed fishery, fishing mortality rates, Bayesian, Atlantic salmon

Introduction

Fish stocks in mixed-stock fisheries often exhibit different migration patterns, life histories, productivity rates and susceptibilities to natural and fishing mortality rates. This makes it difficult to assess the impact of mixed stock fisheries on the individual stocks. Catch data, catch-per-unit-effort data and research indices of abundance, often applied in stock assessments, may contain sufficient information to assess exploitation rates of the combined population, but due to the level of aggregation, these data are unlikely to provide sufficient information about exploitation rates on the individual stocks (Hilborn 1990; Hampton and Fournier 2001).

In contrast, mark and recapture data, provided that the tagging design is adequate and the reported recapture rates are sufficiently high, can be among the most informative types of data available for fish stock assessment (Punt et al. 2000; Martell and Walters 2002). In this paper we demonstrate how mark-recapture data can be used for the assessment of the exploitation rates of stocks within a mixed stock fishery. Even though the amount of tagging data for small or heavily depleted stocks may be limited, there may exist additional biological information on these stocks, not necessarily expressed quantitatively or as data series. By analysing the mark-recapture data within a Bayesian framework, this additional information can be incorporated to improve assessments of individual fish stocks.

This paper proposes a Bayesian state-space mark-recapture model to estimate the fishing mortality rates of stocks caught within a mixed stock fishery, particularly when data for some of the stocks are sparse. The next, i.e., second, section outlines some of the general aspects of the methodology. The third section provides a background on Atlantic salmon (*Salmo salar*) stocks from the north-eastern rim of the Baltic Sea. This section contains subsections on the data, information about the population biology, the population dynamics model, the observation model and the estimation of exploitation rates. The fourth and fifth sections contain the results, and discussion and conclusions.

Methods

Several review papers have been written related to capture, recapture and removal statistics for the estimation of population size and demographic parameters (Seber 1982; Pollock 1991; Schwarz and Seber 1999). The early mark-recapture models applied in fisheries used explicit maximum likelihood estimates when fitting a model to tagging data (Seber 1982). The use of mark-recapture methods within a Bayesian context is more recent (Gazey and Staley 1986; Newman 2000; Mäntyniemi and Romakkaniemi 2002). Bayesian methods allow researchers to use both quantitative data and qualitative information that may be obtained from experts (expert opinions) or from previous studies (prior knowledge) (Malakoff 1999). This makes the Bayesian approach particularly useful in situations when data are sparse and the associated uncertainty in population parameters is large (Ludwig et al. 2001). The problem of sparse tagging data series is common in fisheries since most mark-recapture experiments are done on an opportunistic basis, rather than based on careful tagging experiments designed to facilitate ongoing fisheries stock assessments (Martell and Walters 2002). Within this paper a Bayesian mark-recapture model is proposed to estimate the fishing mortality rates of stocks (including data-poor ones) within a mixed fishery. The Bayesian approach explicitly deals with uncertainty, i.e., uncertainty in the parameter values and uncertainty in the observations or data (Punt and Hilborn 1997). Natural variability in the population dynamics is accounted for by applying a state-space formulation of the mark-recapture model (Rivot et al. 2004).

The mark-recapture model consists of a population dynamics model, describing the dynamics of the population of interest, and an observation model, describing how the recapture data have been obtained (McAllister et al. 1999). The mark-recapture model uses prior probability density functions (pdfs) for model parameters such as population parameters (natural mortality rates, maturation rates and/or migration rates), fisheries related parameters (catchability coefficients), data collection parameters (tag reporting rates) and for parameters that convey process error in system dynamics and observation error in the data. These prior pdfs reflect the prior beliefs about the values for these parameters and can be used together with the data in Bayes' theorem to compute the joint posterior density function of the state-space model parameters or the Bayesian probability that the parameter values are true given the recovered tags (Gelman et al. 1995). The joint posterior density function therefore states the degree of belief in values of state-space model parameters given the mark-recapture data. In order to avoid possible confounding of the reporting rates with other parameters, the tag reporting rate priors are not updated by the tagging data.

The Bayesian mark-recapture analysis is run using WinBUGS (Bayesian inference Using Gibbs sampling) software (http://www.mrc-bsu.cam.ac.uk/bugs), version 1.4. WinBUGS uses MCMC (Markov Chain Monte Carlo) methods to sample from the posterior probability density function (Thomas et al. 1992). All of the modelling results described in this paper have undergone tests to remove the 'burn-in' associated with the use of MCMC methods and to assess convergence (Best et al. 1995). It is therefore assumed that the reported distributions are representative of the underlying stationary distributions. In addition, the fit of the model to the data has been assessed by comparing the data to the posterior predictive distribution of the model i.e. the distribution of data simulated from the model (Gelman et al. 1995; Michielsens and McAllister 2004). The result of this comparison can be expressed in terms of a Bayesian p-value (Meng 1994). Bayesian posterior predictive p-values indicate the probability that the replicated data could be as extreme or more extreme than the observed data. Alternative model structures have been compared using the Deviance Information Criterion (DIC), which is a Bayesian measure of model complexity and fit (Spiegelhalter et al. 2002). The model that best replicates the data will have the smallest DIC.

Application: estimation of the exploitation rates of Atlantic salmon (Salmo salar) stocks in the Baltic Sea

Wild Atlantic salmon stocks are exploited in the Baltic Sea by a sequence of six salmon fisheries. While foraging in the Baltic Main Basin, salmon are captured by offshore driftnet and offshore longline fisheries. Upon maturing, they migrate back to the rivers to spawn. During their migration they may be captured by coastal driftnet, coastal trapnet or coastal gillnet fisheries or by the river fishery, consisting predominantly of rod fishing. Trends in wild salmon abundance cannot be ascertained from catch and fishing effort data because of the large numbers of hatchery-reared salmon stocked annually in the Baltic Sea and the paucity of records on the fraction of wild fish in annual catch records (Karlsson and Karlstöm 1994; Romakkaniemi et al. 2003).

Data

Between 1987 and 2003, about 27000 wild salmon smolts have been tagged from the rivers Tornionjoki and Simojoki, which are located at the north-eastern rim of the Baltic Sea (Figure 1) (ICES 2005). Recapture records have been obtained for each of the main fisheries in the Baltic Sea area. With a tag recovery rate of 5.6 %, the annual number of wild salmon tag recoveries is relatively low, especially given the lack of tagging in 1989-90 and 1995-97.

Figure 1

The mark-recapture model therefore relies also on tagging data from related hatchery-reared salmon stocks of the neighbouring rivers Iijoki and Kemijoki to facilitate parameter estimation for wild salmon stocks (ICES 2005). It is assumed that these hatchery-reared salmon stocks have similar sea migration patterns, i.e., to the feeding grounds at the Main Basin and back to the spawning rivers (Romakkaniemi et al., 2003), and similar biological characteristics as wild salmon stocks, with the exceptions specified in the next section. For simplicity it is assumed that the wild stocks of the two rivers do not differ from each other nor do the two hatchery-reared stocks differ from each other in any respect relevant for the modelling. A total of around 170000 hatchery-reared salmon smolts have been tagged and released in these rivers between 1987-2003 (ICES 2005).

In addition to the tagging data, the mark-recapture model also uses fishing effort data as a covariate for fishing mortality rates (Figure 2). This reduces the number of estimated parameters and may increase efficiency in parameter estimation (Seber and Schwarz 2002).

Figure 2

The unit of fishing effort is in gear-days (number of units of gear deployed (e.g. long line hooks) x number of days deployed per year) (ICES 2005). Since the mid-nineties, fishing effort on salmon in the Baltic Sea has decreased markedly. Since the mid-eighties about 10% of the annual catch has been taken by river anglers. In absence of annual river fishing effort data, only the long-term average fishing mortality rate in rivers can be estimated using a single constant value for river fishing effort. Tables containing the data can be found in the ICES working group reports for the assessment of Baltic salmon and trout (ICES 2002; 2005).

Information on the population biology of wild and hatchery-reared stocks

In addition to the mark-recapture data, there exists tagging independent information about the life history characteristics of wild salmon stocks, especially in relation to their hatchery-reared counterparts, e.g., the differences in age of maturation and in natural post-smolt mortality (Salminen et al. 1995; Kallio-Nyberg and Koljonen 1997; Jutila et al. 2003). It is of interest to find methods to incorporate such basic biological knowledge into stock assessments (Ulltang 1996). This information has played a key role in the specification of the model structure and the prior pdfs of model parameters.

Tagging data for both wild and hatchery-reared salmon are analysed together whereby the model structure describes the relationship between certain parameters for wild and hatchery-reared salmon. The maturation rate for wild grilse is assumed to be lower than for hatchery-reared grilse due to the lower growth rate (Kallio-Nyberg and Koljonen 1997; Jutila et al. 2003). This is implemented by multiplying a mean maturation rate for grilse respectively with a yearly maturation effect for wild or hatchery-reared salmon. Maturation rates for wild grilse are thereby allowed to be the same or smaller than maturation rates for hatchery-reared grilse. In addition, the post-smolt mortality rate of hatchery-reared salmon is assumed to be higher than that of wild salmon (Olla et al. 1998; Brown and Laland 2001). This is implemented similarly as for the maturation rates. The post-smolt mortality rates are allowed to differ from year to year (Salminen et al. 1995), and it assumed that these annual changes are the same for both wild and hatchery-reared salmon. Unlike the post-smolt mortality rate, the instantaneous natural mortality rate for adult salmon is assumed to be constant over the years and the same for wild and hatchery-reared salmon.

Existing information about the salmon stocks is also incorporated by assigning prior pdfs to biological model parameters. The prior pdfs for these parameters are obtained through the use of expert knowledge about biological parameters for Atlantic salmon in general or Baltic salmon in particular. When depending on expert judgment it is better to depend on a group of experts (Punt and Hilborn 1997) and keep the methods to elicit prior information as simple as possible (Chaloner 1996). For the analysis in this paper, twelve experts have been asked to provide the most likely value and a minimum and maximum value for the biological model parameters based on previous studies and relevant literature. Care has been taken to ensure that the expert judgment is not based on data used within the mark-recapture model to avoid using the same data twice and thus rendering the results too informative. The use of multiple experts resulted in multiple priors for the different biological parameters. Each expert was given the same weight when combining the priors from the different experts through arithmetic pooling (Genest and Zidek 1986; Spiegelhalter et al. 2004). An overview of the different model parameters and their prior pdfs is provided (Figures 3 and 4) as well as a list of all the symbols used for the different model parameters (Table 1).

Figure 3

Figure 4

Table 1

Population dynamics model

The population dynamics model used within the mark-recapture analysis is age-structured and assumes that all salmon are the same smolt age when tagged and released. The offshore driftnet fishery (DF), offshore longline fishery (LF), coastal driftnet fishery (CDF), coastal fishery (CF) and river fishery (RF), are assumed to take place during sequential points in time (Figure 5). The population dynamics equations are of the following general form

Figure 5

(1) $$N_{r,t_2,a} = N_{r,t_1,a} e^{-F_{f,y,a} - \Delta t\, M_{y,a}/12} \varepsilon_{y,t}$$

whereby $N_{r,t,a}$ is the abundance of tagged salmon in month *t* during their a^{th} year at liberty after release in year *r* and $F_{f,y,a}$ is the instantaneous fishing mortality rate by fishery *f* in year *y* whereby y = r + a –1. $M_{y,a}$ is the instantaneous natural mortality rate in year *y*. During their first year at liberty, salmon experience high natural mortality rates when migrating from the freshwater environment to sea (Salminen et al. 1995). The natural mortality rate during the first year at liberty i.e. the post-smolt mortality ($M_{y,1}$), is therefore different from the adult mortality rate which is assumed to be the same for different age groups (a = 2 to 4) and across years. Because equation 1 covers $t_2 - t_1 = \Delta t$ months, the yearly instantaneous natural mortality rate is adjusted to cover the same period ($\Delta t \cdot M_{y,a}/12$). In the coastal areas, it is assumed that the percentage of salmon mauled by seals has increased annually by 5.5% between 1995 and 2001, following the increase in the seal population (ICES 2002). In coastal areas, an additional seal related mortality factor ζ_y is used to increase the instantaneous natural mortality rate above the average rate.

The population dynamics model includes four different life history types that spend from one to four winters at the sea before returning to the rivers to spawn. Assuming tagged smolts migrate to sea immediately after being released, the number of years at liberty corresponds to the number of years at sea. Each year, a fraction of the salmon population will mature (L_a) and start migrating back to the river,

(2) $$N_{r,t_4,a+1} = L_a N_{r,t_3,a} e^{-F_{f,y,a} - \Delta t \cdot M_{y,a}/12} \varepsilon_{y,t}$$

while the immature salmon will remain another year at sea

(3) $$N_{r,t_5,a+1} = (1 - L_a) N_{r,t_3,a} e^{-F_{f,y,a} - \Delta t \cdot M_{y,a}/12} \varepsilon_{y,t} \ .$$

Salmon that return after 1 winter at sea are called 1-Sea-Winter (1SW) salmon or grilse. In case they remain several years at sea before spawning, they are named Multi-Sea-Winter (MSW) spawners. It is assumed that all salmon die after spawning. Wild and hatchery-reared salmon are modelled as separate fish stocks without causal dependencies, even though some of their life history parameters are linked in the sense that knowledge from the hatchery-reared population is assumed to help in the assessment of wild salmon.

Deviations from the population dynamics model predictions are modelled within each survival process by including a process error term $\varepsilon_{y,t}$. In the absence of data, a symmetrical uniform distribution around 1 is proposed for the process error in survival rates, whereby the variance of the process error is made dependent on the size of the time step and on the mortality rate Z. In general, state-space models use yearly time steps when modelling a population. Because of the importance of within-year detail when modelling migratory species exploited by several different fisheries, smaller than yearly time steps may be required. Assuming that variance components are additive, the variance of the yearly process error is divided by 12 and multiplied by the number of months over which the process error is applied. The smaller the time steps, the smaller the variance.

In addition to the time-steps, the process error is also dependent on the total mortality rate Z, based on the assumption that without recruitment, the product of the total survival rate e^{-Z} and the process error ε_t should be smaller than 1 ($0 < N_{t+1} = N_t e^{-Z} \varepsilon_t < N_t$ *and* $e^{-Z} \varepsilon_t < 1$). By definition, the process error will therefore be larger than 0 and smaller than e^{Z}. Because the uniform prior pdf is assumed to be symmetrical around 1, the value closest to 1 will determine the minimum and maximum value of the uniform distribution. At each point during the life history, the process error is assumed to be the same for wild and hatchery-reared salmon. In case wild and hatchery-reared salmon have different survival rates, the smallest resulting process error is applied to both.

This proposed process error term differs significantly from earlier process error terms such as the one of Schnute and Richards (1995),

(4) $$\varepsilon_t = \frac{e^{\sigma\delta}}{1 - e^{-M} + e^{-M} e^{\sigma\delta}}$$

which is derived from independent standard normal variates δ, natural mortality M, and a parameter σ related to the variance of ε_t. This process error term can be adjusted to be dependent on the total mortality rate. The process error of Schnute and Richards (1995) has a more pronounced peak around one compared to the formulation proposed in this paper. A flatter process error term accounts for more uncertainty in system dynamics and allows data to update the process error term more readily. When using the new process error term within the mark-recapture model, the WinBUGS program runs more than four times faster than when using the process error term of Schnute and Richards (1995), due to faster mixing MCMC chains. The new process error formulation thus appears to provide advantages over existing alternatives.

Observation model

The number of reported tags under-represents the total number of tagged salmon caught because a proportion of the recaptured tags remains unreported. Several analyses have been undertaken to try to estimate the tag reporting rates in the different salmon fisheries of the Baltic Sea (ICES 2003). In general, these analyses are based on certain fishermen or certain fleets and only give a first indication of the possible reporting rates in the different fisheries. Expert judgment is used to extrapolate the resulting reporting rates to the entire fisheries or to other fisheries, as experts are believed to have information about fisheries which is not directly available from existing data sets.

Expert judgment about the tag reporting rates by fishermen of their national fishing fleet was elicited from twelve experts. The experts based their judgments on data obtained from these studies, information from literature and their own experiences and observations. The expert information was obtained in the same way as for biological parameters but was combined by weighting the pdfs for each nation by the nation's contribution to salmon catches (Table 2). This reflects the assumption that reporting rates of tags are dependent on the country of origin of the fishermen and that experts only have knowledge of reporting rates by fishermen from their own country. Reporting rates and tag shedding rates for the offshore driftnet fishery and the coastal driftnet fishery are assumed to be the same.

Table 2

The expected number of tags caught and reported by the different fisheries during the salmon's a[th] year at liberty is therefore given by the following equation

(5) $$C_{f,r,a} = \gamma_f \lambda_f \varphi_f N_{r,t,a} e^{-F_{f,y,a} - M_{y,a}/24}$$

whereby $C_{f,r,a}$ is the expected number of caught and reported tags from salmon released in year *r* and recaptured after *a* years at liberty by fishery *f* in the middle of the month (M/12/2),

γ_f is the probability that the fishermen will report the tags when recaptured by fishery *f* and λ_f is the probability that the salmon will retain the tags when caught by fishery *f*. Tag retention problems are assumed to occur only when catching the tagged salmon with driftnets. In order to account for tagged salmon removed from traps or nets by seals, a factor φ_f is used to adjust the reporting rate of tags recaptured by the coastal fishery. This adjustment factor should decrease the reporting rate of the coastal fishery annually by 5.5% between 1995 and 2001.

It is assumed that the reported tags are distributed according to a negative binomial distribution, taking into account the schooling behaviour of the salmon (Christensen and Larsson 1979) and the somewhat patchy distribution of the total fishing effort. The following version of the negative binomial probability density function (pdf) was used for the probability that the number of recaptured and reported tagged fish equals *c*, given a particular set of model parameters (*θ*),

$$(6) \qquad p(c|\theta) = \frac{\Gamma(k+c)}{\Gamma(k)c!}\left(\frac{k}{k+m}\right)^k\left(\frac{m}{m+k}\right)^c .$$

In this equation *m* represents the sample mean, i.e., the model-predicted number of tagged fish reported in a given fishery in a given year, and *k* represents the overdispersion parameter (Hilborn and Mangel 1997). It is important to note, that the overdispersion parameter has a direct biological explanation: it represents the propensity for schooling behaviour in salmon. Parameter *k* is therefore assumed to be the same across the years but to differ across fish stocks and fisheries. The variance in *c* given *θ* is determined through the equation

(7) $$Var(c) = m + \frac{m^2}{k}.$$

The larger the value of the overdispersion parameter, the closer the approximation to a Poisson distribution. Both the recaptured and reported hatchery-reared tagged salmon as well as the recaptured and reported wild tagged salmon are assumed to follow a negative binomial distribution.

Estimation of the exploitation rates

The main outputs of the model are the fishing mortality rates or exploitation rates which are dependent on the fishing effort ($E_{f,y}$) and the catchability coefficients ($q_{f,a}$) of the different fisheries, according to the following equation

(8) $$F_{f,y,a} = q_{f,a} E_{f,y}.$$

The uncertainty over values for catchability plays a key role within assessments when effort based management systems are applied. The catchability coefficients, $q_{f,a}$ or q, have been estimated independently for different age groups in case the fisheries have different efficiencies to catch different age groups as assumed to be the case for the driftnet, trapnet and gillnet fisheries. It has been assumed that q can vary between different fisheries, and between different age groups of wild and reared salmon and that there is an underlying distribution for q across these groups. This has been implemented within the model by assuming a hierarchical model structure defined through a mean catchability coefficient of fishery f for fish of age a for the combined set of stocks ($\mu_{q,f,a}$) and a cross-stock variance of the catchability coefficients ($\sigma^2_{q,f,a}$) (Gelman et al. 1995; Millar and Methot 2002). An overview of the estimated catchability coefficients for the different fisheries can be found in Figure 4.

Selecting appropriate prior pdfs for these parameters can be difficult. Non-informative prior pdfs for the catchability coefficients may result in bimodal distributions for the corresponding harvest rates with peaks at 0 and 1. Therefore priors are placed on the harvest rates for each fishery in the first year of the data series, i.e., 1987 ($H_{f,y=1987,a}$), and based on the fishing efforts during that year, the prior pdfs for the corresponding catchability coefficients are calculated.

(9) $$q_{f,a} = \frac{-\log\left(1 - H_{f,1987,a}\right)}{E_{f,1987}}$$

The prior pdf's for the harvest rates in 1987 are given by uniform distributions between 0 and 1, Unif(0, 1). Some tagged salmon are caught incidentally immediately after their release. Even though the associated fishing mortality is assumed to be small, these tagged salmon need to be accounted for in order not to overestimate the survival rate. The prior pdf of the incidental harvest rate during feeding migration is therefore given by Beta(1, 20). In combination with the fishing effort in subsequent years, the prior pdfs for the catchability coefficients determine the prior pdfs for the harvest rates in subsequent years.

For each year the model estimates different harvest rates or fishing mortality rates depending on the fishery, depending on the age of the fish and depending on whether it is a wild or hatchery-reared fish. To present these values at this detailed level of disaggregation would be confusing and not necessarily useful for management purposes. Instead the total cumulative fishing mortality rates are reported for wild or hatchery-reared fish depending on the number of winters (a-1) the salmon stay at sea. This total cumulative fishing mortality rate relates to the total fishing pressure a fish is subjected to during its life history. For example a 2-Sea-Winter (2SW) salmon can be caught by the river and coastal fishery when migrating to the feeding grounds (as a non-target species of miscellaneous types of fisheries), by the driftnet and longline fishery during its first and second winter at sea, by the coastal driftnet, trapnet and gillnet fishery during the migration to the spawning grounds and by the river fishery. The general formula for the total cumulative fishing mortality rate for 1SW to 4SW salmon is given by the following equation

(10) $$F_{(a-1)SW,y} = \sum_{f=RF,CF} F_{f,y-a+1,1} + \sum_{f=DF,LF} \sum_{a} F_{f,y-a+1,a-1} + \sum_{f=CDF,CF,RF} F_{f,y,a} \text{, with a = 2 to 5.}$$

The total cumulative fishing mortality rate thus spans the entire life history of the salmon and it shows directly how large the impact of fishing is on the spawning capacity compared to an unexploited situation. The total cumulative fishing mortality rates only reflect the mortality due to fishing and do not include any natural mortality. To simplify the interpretation of the results, cumulative fishing mortality rates are expressed as total harvest rates.

Results

The prior pdfs of model parameters for hatchery-reared salmon have been updated considerably due to utilizing informative tagging data for reared salmon (Figures 3 and 4). For wild salmon, the prior pdfs for the maturation rates and natural mortality rates, have been updated to a lesser extent because the priors had already been quite informative and the information available in the tagging data for wild salmon was limited. The annual posterior estimates for the post-smolt mortality rate of wild and reared salmon are shown in Figure 6.

Figure 6

There is a trend in the results indicating that post-smolt mortality rates have been higher in recent years. The reasons for this shift in post-smolt mortality rates are still unclear but may be linked to environmental factors (Kallio-Nyberg et al. 2004).

The main outputs of the model are the marginal posterior pdfs for total harvest rates for the different life history types (Figure 7) based on the catchability coefficients of the different fisheries for different age groups. The priors for the catchability coefficients and the derived priors for the harvest rates have been updated considerably due to the information contained in the tagging data and the fishing effort data. The longer the salmon stay out at sea, the higher the chance that they will be captured by the fishery and the higher the corresponding harvest rate. The total harvest rates for 2SW wild salmon have been compared to the preliminary precautionary reference point (ICES 2002). The total harvest rate of 2SW wild salmon is higher than the precautionary reference point for 2SW salmon, indicating that from a fisheries management perspective exploitation rates are too high.

Figure 7

Several diagnostic measures have been calculated. The posterior predictive distribution of model quantities indicates whether the model's predictions are plausible given the observed data. About 1.8% of the observed data points were located outside the 95% probability intervals of the posterior predictive distributions. This indicates that the data could have been obtained from the model and the posterior pdfs of model parameters. When calculating Bayesian p-values, data points with a value of 0 have been excluded. These data points would result in Bayesian p-values of 1 when assuming a negative binomial likelihood function. For the remaining data points, only 2.6% of the posterior predictive p-values are larger than 0.975 and 2.1% are smaller than 0.025.

One of the main concerns when using tagging data in stock-assessments is the uncertainty regarding the tag return rates (Hilborn and Walters 1992). In this paper, the tag return rate parameters (i.e., tag reporting and retention rates) have been based on partial data, extrapolated through expert judgement. In order to assess the impact of the choice of the prior pdfs for the tag reporting and retention rates on the resulting estimates for the exploitation rates, three different scenarios have been compared against the base case. First it has been assumed that less information was available regarding the tag return rates resulting in less informative prior pdfs. This has been implemented by doubling the CV of the prior pdfs for the tag return rate parameters. Secondly more informative prior pdfs with half the original CV's have been specified in order to assess the benefit of investing in studies to provide more precise estimates of parameters determining the tag return rates. Thirdly, the parameters determining the tag return rates have been given prior pdfs with different means, assuming the means of the pdfs for the tag return rate parameters are one third lower than under the base case scenario.

The resulting probability density functions for the cumulative harvest rate of 2SW fish returning in 2004 are presented (Figure 8, panel a). The four posterior pdfs overlap but there are distinct differences between them. As could be expected, less informative prior pdfs for tag return rates result in a wider posterior pdf for the total harvest rate with a higher probability of very high total harvest rates. More informative prior pdfs for tag return rates result in slightly more informative estimates of the exploitation rate. When tag return rates are assumed to be lower than was the case for the base case scenario, the total harvest rate needs to be higher in order to obtain the same number of reported tagged salmon in the catch. In general it can be concluded that the amount of uncertainty in the prior pdfs of parameters determining the tag return rates has a clear impact on the uncertainty in the estimates of the total fishing mortality rate. Greater uncertainty in these prior pdfs will result in higher estimates of the total cumulative exploitation rates. This would lead to more restrictive fisheries management advice. These arguments underline both the importance of including uncertainty in the values used for tag return rates and the importance of investing in studies to reduce as much as possible the uncertainty in the prior pdfs for the tag return rates. Such studies could include scientific observer programs and high reward tagging studies. Similar sensitivity analyses for the maturation rates and natural mortality rates (Figure 8, panel b and

Figure 8

c) indicate the limited impact of the priors pdfs for the maturation rates and natural mortality rates on the posterior probability distributions for the harvest rates.

The use of a negative binomial likelihood function was compared to alternative model structures that use Poisson, binomial and beta-binomial pdfs for the reported tags. The Poisson distribution is a special case of the negative binomial distribution, obtained by assuming a random spatial and temporal distribution of fish and reported tags instead of a clustered distribution. The beta-binomial pdf is more realistic than the negative binomial distribution because it assigns zero probability to catches higher than the number of tagged fish. When tag return probabilities are low, the beta-binomial pdf approximates the negative binomial distribution. The binomial distribution is a special case of the beta-binomial distribution that assumes a random spatial and temporal distribution of fish and tags. The DIC for the scenario based on negative binomial likelihood functions was 4315 while the DIC for the models using Poisson, binomial or beta-binomial pdfs for the likelihood functions were 6287, 6641 and 4468 respectively. This indicates that models assuming a clustered distribution of fish obtain a better fit to the mark-recapture data than models assuming a random distribution. The model using the negative binomial distribution gives a slightly better fit to the mark-recapture data than the model assuming a beta-binomial distribution. When calculating the DIC, no negative values have been obtained for the effective number of parameters, suggesting there is no indication of conflicts between the priors and the data or of problems related to the parameterisation of the model.

Discussion

We have demonstrated that when reported recapture rates are sufficiently high (e.g., > 5%), as in the case of salmon fisheries, mark-recapture analyses can allow for the estimation of annual fishing mortality rates. Yet, few fishery stock assessments actually use the tagging data in mark-recapture analyses and take advantage of the fact that mark-recapture analyses do not necessarily need catch or catch-per-unit-effort data. Many fisheries stock assessments however use tagging data to examine stock structure (Kohler and Turner 2001), movement or migration patterns (Sibert et al. 1999; McGarvey and Feenstra 2002) and the allocation of quotas (Caron et al. 2002). Tagging data are currently also used in a number of instances to help estimate harvest rates on fish stocks. For example, the incorporation of tagging data in MULTIFAN-CL (Hampton and Fournier 2001), a methodology which analyses length-frequency distributions of catches, facilitates the estimation of harvest rates. Mark-recapture data are also analysed using conventional mark-recapture methods (e.g., Jolly-Seber) to help estimate harvest rates for some stocks, for example, individual Canadian Atlantic cod stocks (Cadigan and Brattey 2002) and north-east Atlantic mackerel (Skagen 2003). In contrast, this paper has presented a Bayesian state-space methodology to estimate harvest rates on individual stocks imposed by a sequence of mixed-stock and single stock fisheries.

One of the main factors constraining the use of tagging data for stock assessment purposes is the uncertainty over reporting rates of tags by fishermen (Hilborn and Walters 1992). By analysing tagging data within a Bayesian setting, the uncertainty regarding the reporting of tagged fish can be taken into account. The information for the probability distributions of the reporting rates can be obtained from studies designed to estimate the reporting rates, from expert opinion or a combination of the two. Using this approach, mark-recapture analyses can provide estimates of exploitation rates independent from catch data. By incorporating mark-recapture analyses in conventional fisheries stock-assessments (Patterson 1999; Punt et al. 2000), the results become more robust (Martell and Walters 2002).

In contrast to many other Bayesian state-space formulations, this paper follows a different convention in which the prior is not placed on the state variable, e.g., abundance (Millar and Meyer 2000), but instead on the process error term itself. This latter convention has already been implemented in a number of papers (McAllister et al. 1994; McAllister and Ianelli 1997). By placing priors on the process errors terms, $\varepsilon_t \sim \mathrm{Norm}(0,s^2)$, rather than on the state variable, $N_t \sim \mathrm{logNorm}(fn(N_{t-1}),s^2)$, the computational efficiency and convergence properties improve due to removal of the highly correlated state variables from the set of parameters estimated by the MCMC algorithm (Cunningham 2002).

The survival rate process error model also offers an alternative functional form for the survival rate process error that efficiently keeps to the constraint that $N_{t+1} \leq N_t$. Schnute and Richards' (1995) process error formulation keeps to the same constraint but is computationally less efficient. Lewy and Nielsen (2003) offer a lognormal process error term for survival rate processes. This density function however needs to be truncated to prevent $N_{t+1} > N_t$ and produces more positively skewed density functions than the other two.

For the assessment of mixed-stock fisheries, conventional datasets such as catch data and catch-per-unit effort data offer little information on the individual stocks. Mark-recapture data can provide this kind of information. However, tagging data are often more sparse for overexploited stocks than for more abundant stocks. The Bayesian approach taken facilitates the estimation of exploitation rates of stocks within mixed stock fisheries, even when data are sparse. The methodology utilizes knowledge about key differences and similarities between the fish stocks of interest and biological information about the individual fish stocks based on published literature, expert judgment. This prior knowledge is combined with tagging and effort data to help estimate exploitation rates of each of the fish stocks.

The use of data from similar or related populations is a well-known concept within ecology where data from similar populations are combined within meta-population analyses in order to estimate their population parameters and predict the parameters for unsampled populations (Gurevitch et al. 2001). The dependence among parameters that vary predictably among populations can be modelled though the use of a hierarchical model structure (Gelman et al. 1995). Within this paper, hierarchical structures have been used to model stock dependent catchability coefficients (q). The use of an hierarchical structure however requires that the individual stocks are exchangeable i.e. that the differences between the individual stocks should be unpredictable (Gelman et al. 1995). For the example presented within this paper, this might be the case for the efficiency of the fisheries to catch different stocks. This is not the case for other model parameters where prior information about the stocks already dictates that the model parameter of one stock cannot be larger than the model parameters for another stock. In such cases, it is more appropriate to use an additional parameter, indicating the difference between the parameter values for both stocks.

The use of prior information is an integral part of Bayes' theorem (Gelman et al. 1995). However, some scientists believe that the use of subjective priors, e.g., those derived from experts, is inappropriate and unscientific because these priors may be incorrect or biased (Cox and Hinkley 1982). To reduce the impact of subjective beliefs, the use of uninformative (e.g., flat or low gradient) priors has often been recommended (Walters and Ludwig 1994). An uninformative prior for particular parameters may however lead to informative priors for other variables of interest and, when data are relatively uninformative, this may lead to results that are inconsistent with biologists' understanding about the population (Punt and Hilborn 1997). Uninformative priors for q for example may lead to informative and spurious priors for the associated harvest rates. In contrast, and as demonstrated in this paper and others (e.g., McAllister et al. 1994), the use of informative priors that have been carefully constructed using available knowledge and data other than those to which the model has been fitted will lead to more scientifically credible and defensible results. Therefore management actions can more easily be justified in a precautionary context whereby the increases in uncertainty can help to justify more restrictive management advice.

When applying the assessment methodology to Baltic salmon stocks, links have been built between the life history parameters of wild and hatchery-reared stocks. Although wild and hatchery-reared salmon have somewhat different life histories (Kallio-Nyberg and Koljonen 1997; Jutila et al. 2003), certain population parameters can be regarded as similar or related while others are assumed to differ. In the current model it has also been assumed that within the group of wild stocks and within the group of reared stocks there are no differences in biological characteristics or in harvesting patterns. In our example, the rivers are located next to each other, and the same stock (Iijoki salmon) has been partly used for releases in both of the dammed rivers. The findings of Järvi (1938; 1948) indicate that the differences in the characteristics of the salmon stocks within the groups in the study area are relatively small. In this case the impact of this simplifying assumption is likely to be small. When expanding the model to include more stocks, an hierarchical modelling approach should be considered since local adaptations can lead to differences in migration patterns for different stocks within the group of wild or reared salmon (Alm 1934; Power 1981; Jonsson et al. 1991).

In addition there are several simplifying yet incorrect assumptions about the fisheries and stock characteristics. The number of repeat spawners for example has increased over time. During the last few years, up to 15% repeat spawners have been sampled in the river Tornionjoki (Romakkaniemi et al. 2003). The catchability coefficient of the driftnet fishery may also have changed systematically over time (ICES 2003). In addition, the fishing effort is assumed to be known without error (Pollock 2002) and the process errors are assumed independent. At this stage of the methodological development, these facts have not been accounted for within the model.

Within the current example, no catch data have been used because the mark-recapture model only relates to stocks from rivers located in the north-east of the Baltic Sea while the catch data of the mixed stock fishery relate to all Baltic salmon stocks. Because the exploitation rates of salmon stocks differ depending for example on the location of the river where they spawn within the Baltic Sea, it is not possible to extrapolate the results of the exploitation rates to the entire Baltic Sea, and to estimate the salmon abundance based on the total Baltic salmon catch data. Instead abundance estimates could be obtained by linking the current exploitation rates with estimates of wild smolt production, as obtained by Mäntyniemi and Romakkaniemi (2002), in order to estimate the number of salmon returning to the rivers for spawning (ICES 2005). Alternatively, genetic stock identification methods can be used to estimate the proportion of the catch originating from certain groups of stocks (Koljonen and Pella 1997; Koljonen et al. 2004; ICES 2005).

Even without the estimation of wild salmon abundances and even though there are several simplifications in the model, the current estimates of harvest rates are useful for management purposes by comparing the estimates with limit or precautionary harvest rate reference points (ICES 2002; Martell and Walters 2002). Since 2002, the current mark-recapture methodology has been used for this purpose within the ICES working group for the assessment of Baltic salmon and trout (ICES 2002).

Acknowledgements

Denis Rivard, Holger Hovård, Robin Wyatt, Nicky Best, Hendrik Sparholt, Jaakko Erkinaro, Ken Patterson, Ari Leskelä and Brian MacKenzie provided feedback on the mark-recapture methodology, which is gratefully acknowledged. The mark-recapture methodology has been used within the ICES working group for the assessment of Baltic salmon and trout and has therefore benefited from feedback by its members. The comments of two anonymous reviewers have substantially improved the presentation of this work. This research work has been partly funded by EU project 99/064 “Probabilistic modelling of Baltic salmon stocks” and the Swedish National Board of Fisheries.

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Table 1: List of symbols used within the model

	Indices
y	Year
t	Month
r	Release year
a	Years at liberty i.e. years at sea
f	Fishery
	Model parameters
$M_{y,1}$	Instantaneous natural post-smolt mortality rate in year y (year^{-1})
$M_{y,a\neq 1}$	Instantaneous natural adult mortality rate (year^{-1})
L_a	Proportion of salmon that mature after *a* years at sea
$q_{f,a}$	Catchability coefficient or efficiency of fishery *f* to catch salmon during their a^{th} year at sea (geardays^{-1})
$\varepsilon_{y,t}$	Process error term
γ_f	Probability that the fishermen will report the tags when recaptured by fishery *f*
λ_f	Probability that the salmon will retain the tags when caught by the fishery *f*
φ_f	Adjustment factor for the reporting rate in the coastal fishery *f* to account for the tagged salmon removed from the traps or nets by seals
ζ_y	Adjustment factor for the instantaneous natural mortality rate to account for increased predation by seals in coastal areas in year *y*
	Model variables
$N_{r,t,a}$	Abundance of tagged salmon in month *t* of the a^{th} year at liberty after release in year *r*
$C_{f,r,a}$	Expected number of tags caught and reported by fishery *f* during the salmon's a^{th} year at liberty after release in year *r*
$F_{f,y,a}$	Instantaneous rate of fishing mortality in year *y* by fishery *f* on salmon that spend *a* years at sea (year^{-1})
$H_{f,y,a}$	Harvest rate in year *y* by fishery *f* on salmon that spend *a* years at sea
	Data
$E_{f,y}$	Fishing effort by fishery *f* in year *y* (geardays)
$C_{f,r,a}^{obs}$	Observed number of tags caught and reported by fishery *f* during the salmon's a^{th} year at liberty after release in year *r*

Table 2: Summary of tag return rate parameters, their prior probability density functions (pdfs) and the corresponding prior median, coefficient of variation (CV) and 95% probability interval (PI). The pdfs follow the same parameterisation as used within the WinBUGS program. Beta denotes a beta pdf determined by two shape parameters. These pdfs have been truncated (e.g. I(a,b)) to indicate the prior belief that the random variable can not be smaller than a or larger than b.

Parameters	**Distribution**	**Median**	**CV**	**95% PI**
Tag retention rate	Beta(20,8)I(0.5,1)	0.72	0.11	0.55 - 0.86
Tag reporting rate in the river fishery	Beta(16,6)I(0.3,0.95)	0.73	0.13	0.53 - 0.89
Tag reporting rate in the coastal fishery	Beta(11,9)I(0.3,0.8)	0.55	0.19	0.35 - 0.75
Tag reporting rate in the driftnet fishery	Beta(8,4)I(0.2,0.95)	0.68	0.20	0.39 - 0.89
Tag reporting rate in the longline fishery	Beta(10,4)I(0.3,0.95)	0.72	0.16	0.46 - 0.91

Legends to Figures

Figure 1. Migration route of Atlantic salmon stocks (*Salmo salar*) from the rivers Torne (Tornionjoki), Simojoki, Kemijoki and Iijoki in Sweden and Finland. The driftnet and longline fisheries take place predominantly in the Baltic Main Basin while the trapnet and gillnet fisheries take place in the Gulf of Bothnia. The presence of dams in the rivers Kemijoki and Iijoki, which prevents access to spawning grounds, are indicated by lines across the rivers.

Figure 2. Fishing effort of the driftnet, longline, trapnet and gillnet fisheries on Atlantic salmon stocks (*Salmo salar*) between 1987 and 2004. River fishing effort is assumed to be constant over time. The unit of fishing effort is in geardays (number of units of gear deployed x number of days per year).

Figure 3. Overview of the prior (dotted lines) and posterior (solid lines) probability density functions for maturation rates and instantaneous natural mortality rates of 1-3 Sea-Winter (SW) wild and hatchery-reared Atlantic salmon (*Salmo salar*) in the Baltic Sea area.

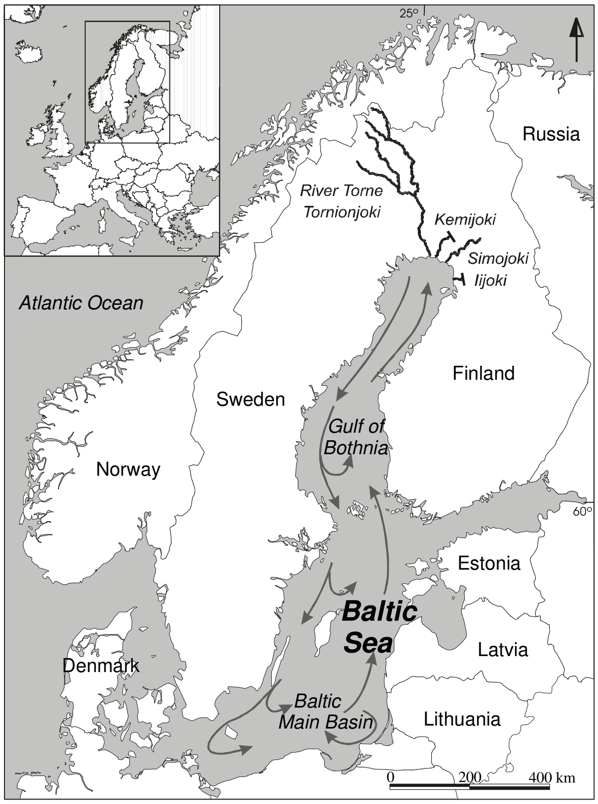
Figure 4. Overview of the prior (dotted line) and posterior probability density functions for the catchability coefficients (10^{-3} geardays^{-1} x year^{-1}) of 1-4 Sea-Winter (SW) wild (posterior – solid line) and hatchery-reared (posterior – dashed line) Atlantic salmon (*Salmo salar*) in the Baltic Sea area by the offshore driftnet and longline fishery, the coastal trapnet and gillnet fishery and the river fishery. The catchability coefficients of the coastal driftnet fishery are assumed the same as for the offshore driftnet fishery.

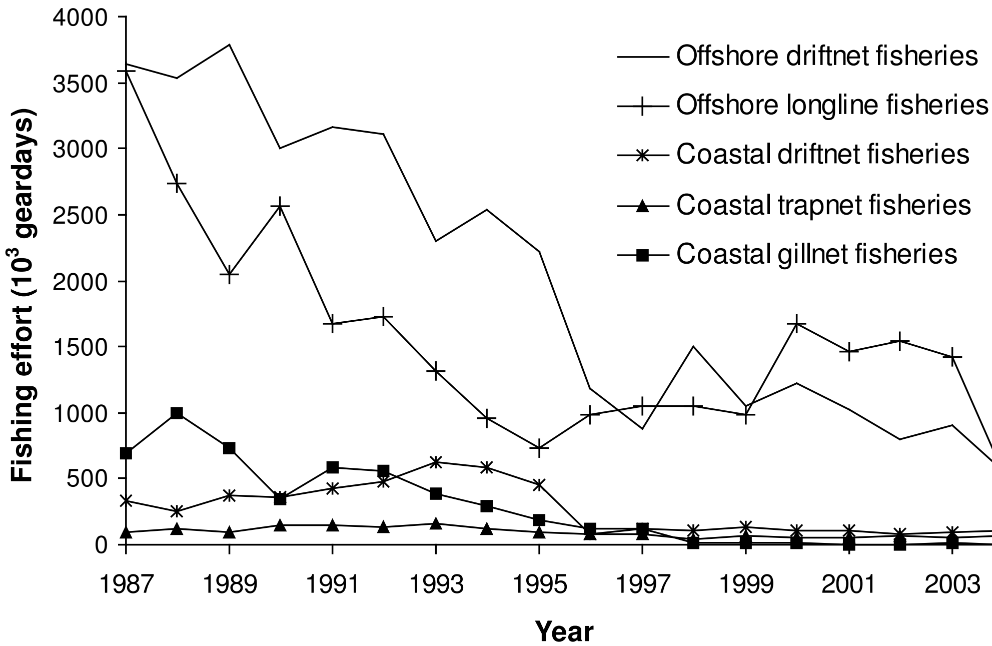
Figure 5. Schematic presentation of the mark-recapture model for Atlantic salmon (*Salmo salar*) in the Baltic Sea area. The offshore driftnet and longline fisheries in the Baltic Main Basin are assumed to take place in October and December respectively. During the migration to the spawning grounds, the salmon can be intercepted by the coastal driftnet fishery in May, the trapnet and gillnet fisheries in June and the river fishery in August.

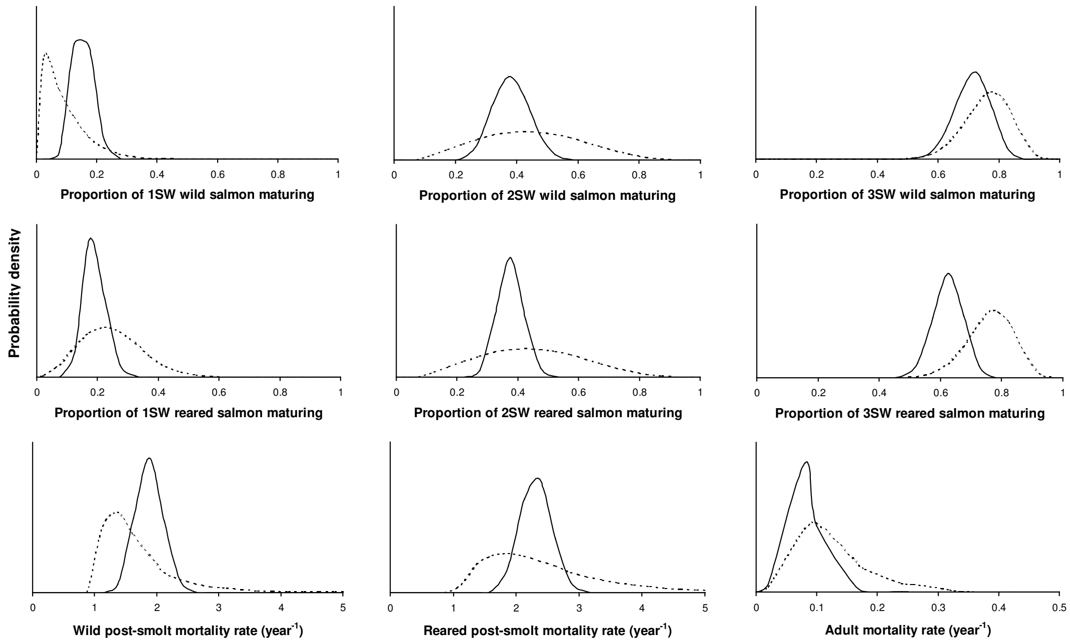
Figure 6. Medians and 95% probability intervals for the annual estimates of post-smolt mortality rates (% per year) for wild and hatchery-reared Atlantic salmon (*Salmo salar*) in the Baltic Sea area between 1987 and 2004.

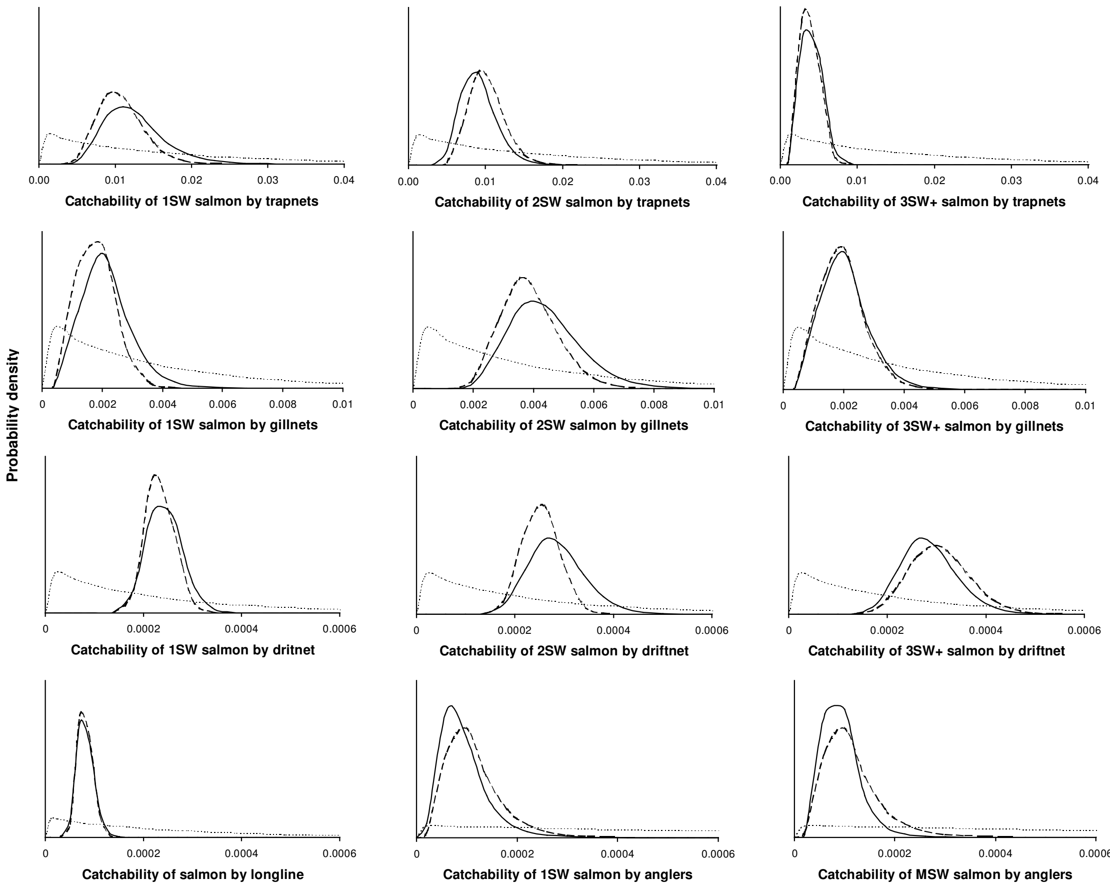
Figure 7. Medians and 95% probability intervals for the total cumulative harvest rate for 1-4 Sea-Winter (SW) wild and hatchery-reared Atlantic salmon (*Salmo salar*) in the Baltic Sea area. The total cumulative harvest rate for 2SW wild salmon can be compared against the precautionary harvest rate reference point (ICES 2002).

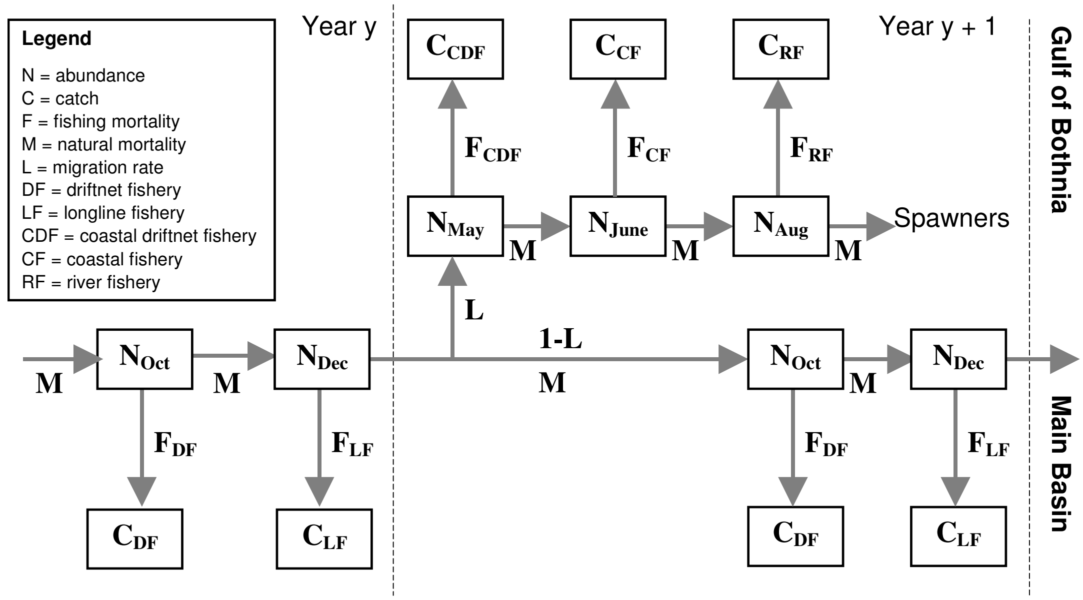
Figure 8. Posterior probability density functions of the total harvest rate for 2SW wild Atlantic salmon (*Salmo salar*) returning to north-eastern Baltic Sea rivers in 2004 when using different prior probability density functions for model parameters determining (a) tag return rates i.e., tag reporting rates and tag retention rates, (b) maturation rates and (c) natural mortality rates.


25°
Russia
River Torne
Tornionjoki
Kemijoki
Simojoki
Iijoki
Atlantic Ocean
Finland
Sweden
Gulf of
Bothnia
Norway
60°
Estonia
Baltic
Sea
Latvia
Denmark
Baltic
Main Basin
Lithuania
0
200
400 km

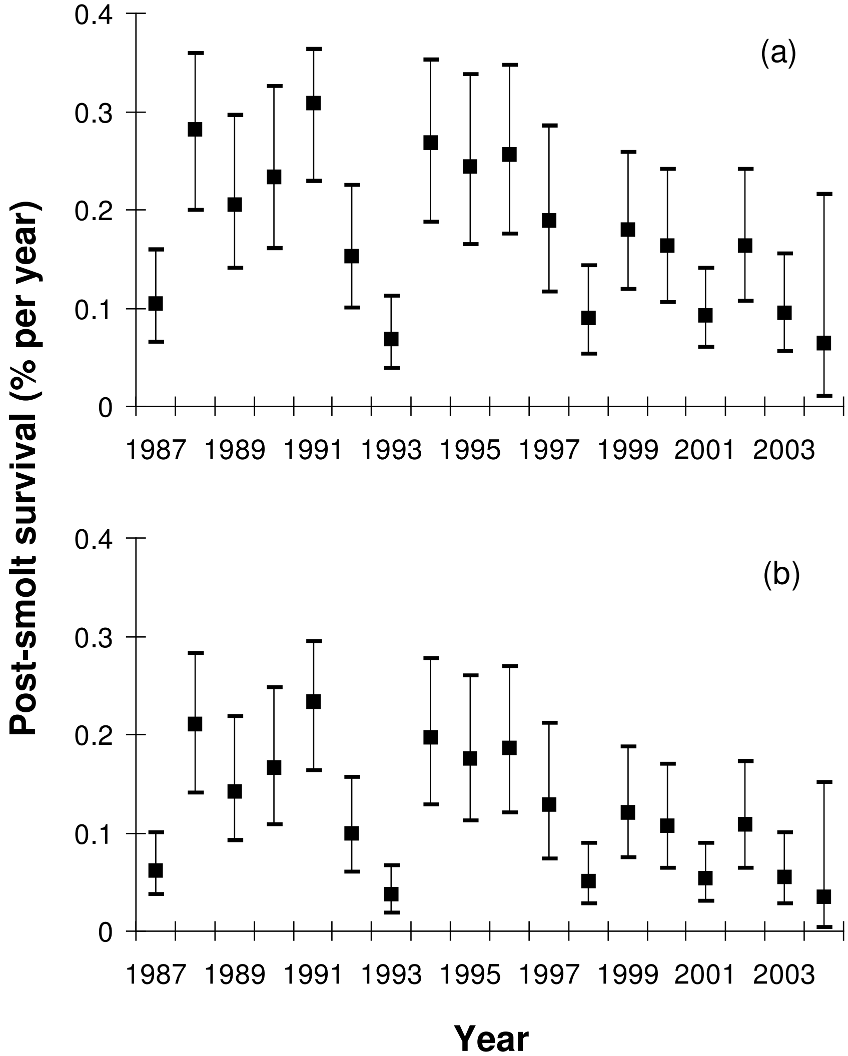

Offshore driftnet fisheries
Offshore longline fisheries
Coastal driftnet fisheries
Coastal trapnet fisheries
Coastal gillnet fisheries
Fishing effort (10^3 geardays)
Year
4000
3500
3000
2500
2000
1500
1000
500
0
1987
1989
1991
1993
1995
1997
1999
2001
2003


Probability density
0
0.2
0.4
0.6
0.8
1
Proportion of 1SW wild salmon maturing
Proportion of 2SW wild salmon maturing
Proportion of 3SW wild salmon maturing
Proportion of 1SW reared salmon maturing
Proportion of 2SW reared salmon maturing
Proportion of 3SW reared salmon maturing
2
3
4
5
Wild post-smolt mortality rate (year^{-1})
Reared post-smolt mortality rate (year^{-1})
0.1
0.3
0.5
Adult mortality rate (year^{-1})

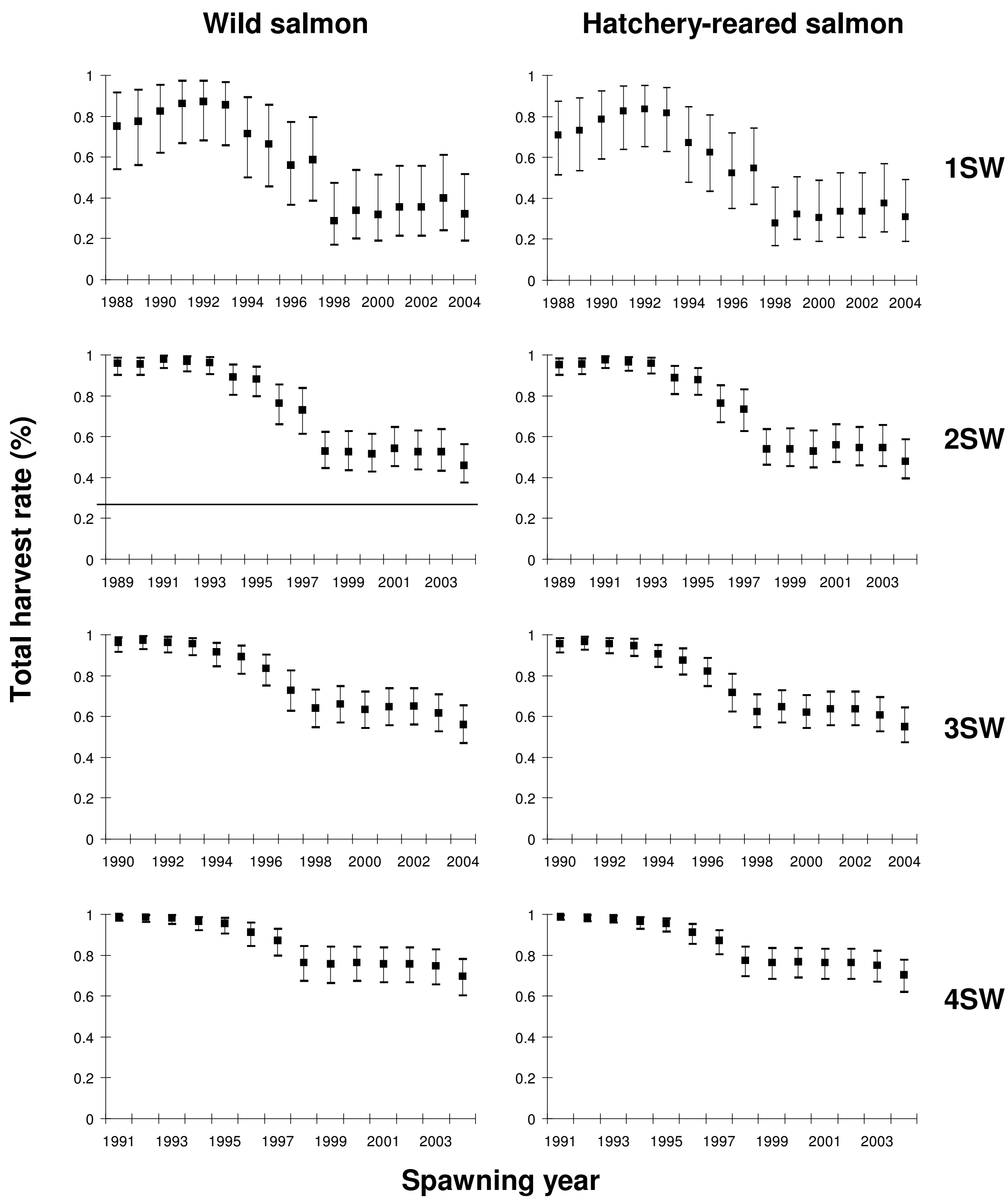

Probability density
0.00
0.01
0.02
0.03
0.04
Catchability of 1SW salmon by trapnets
Catchability of 2SW salmon by trapnets
Catchability of 3SW+ salmon by trapnets
0
0.002
0.004
0.006
0.008
0.01
Catchability of 1SW salmon by gillnets
Catchability of 2SW salmon by gillnets
Catchability of 3SW+ salmon by gillnets
0
0.0002
0.0004
0.0006
Catchability of 1SW salmon by dritnet
Catchability of 2SW salmon by driftnet
Catchability of 3SW+ salmon by driftnet
Catchability of salmon by longline
Catchability of 1SW salmon by anglers
Catchability of MSW salmon by anglers



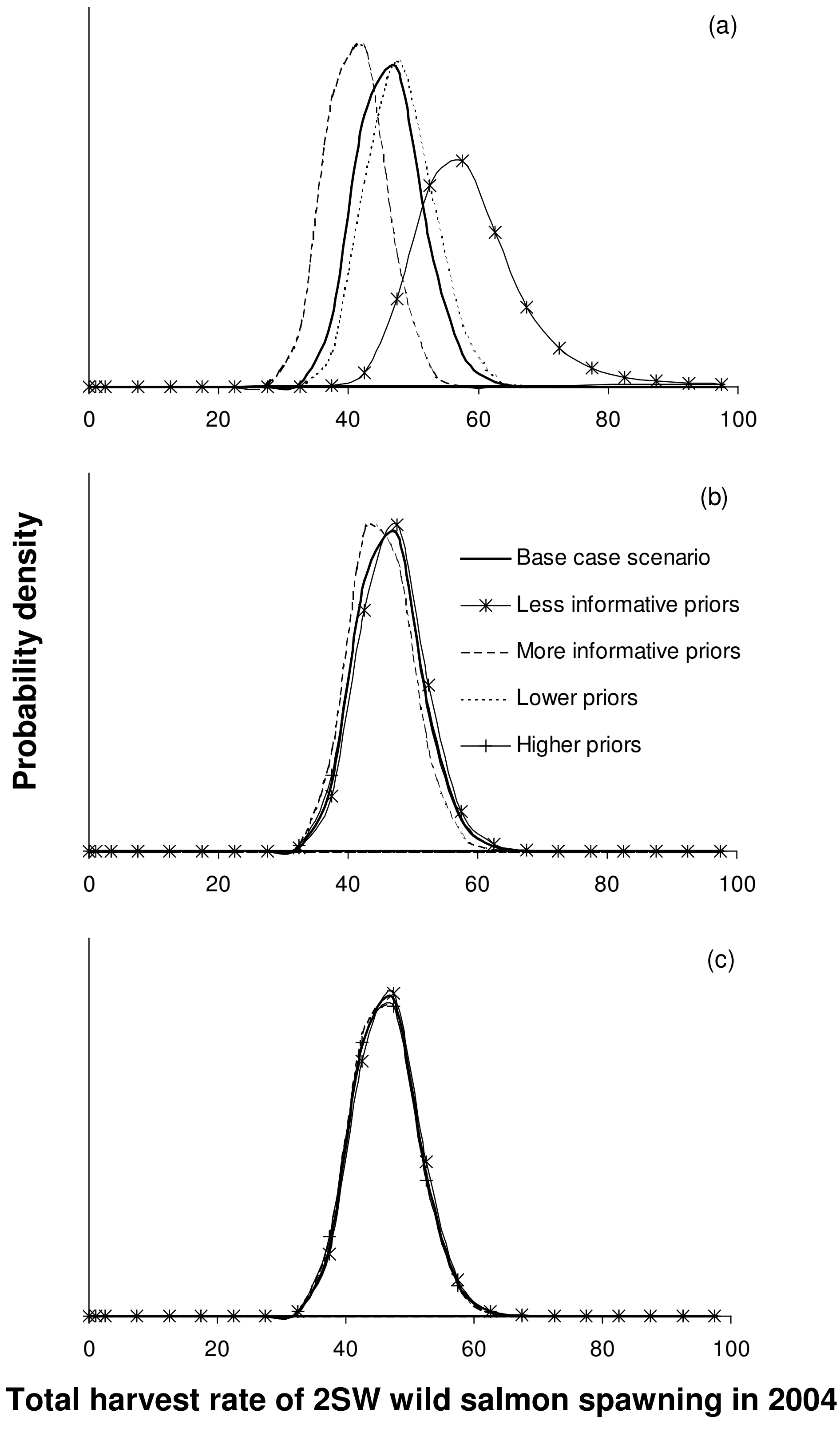
Legend
N = abundance
C = catch
F = fishing mortality
M = natural mortality
L = migration rate
DF = driftnet fishery
LF = longline fishery
CDF = coastal driftnet fishery
CF = coastal fishery
RF = river fishery
Year y
Year y + 1
Gulf of Bothnia
Main Basin
C_{CDF}
C_{CF}
C_{RF}
F_{CDF}
F_{CF}
F_{RF}
N_{May}
N_{June}
N_{Aug}
Spawners
M
L
1-L
N_{Oct}
N_{Dec}
F_{DF}
F_{LF}
C_{DF}
C_{LF}



Post-smolt survival (% per year)
0.4
0.3
0.2
0.1
0
(a)
1987
1989
1991
1993
1995
1997
1999
2001
2003
(b)
Year



Wild salmon
Hatchery-reared salmon
1SW
2SW
3SW
4SW
Total harvest rate (%)
Spawning year


(a)
(b)
(c)
Probability density
Base case scenario
Less informative priors
More informative priors
Lower priors
Higher priors
0
20
40
60
80
100
Total harvest rate of 2SW wild salmon spawning in 2004