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Original Article

Trade-offs among spatio-temporal management actions for a mixed-stock fishery revealed by Bayesian decision analysis

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Management and conservation of populations that are harvested simultaneously present a unique set of challenges. Failure to account for differences in productivity and spatio-temporal abundance patterns can lead to over-exploitation of depleted populations and/or loss of potential yield from healthy ones. Mixed-stock fisheries (where a stock may comprise one or more populations of reared or wild origin) harvest multiple stocks, often in unknown proportions, and lack of tools for estimation of stock-specific harvest rates can hamper status evaluations and attainment of management goals. We present a method for evaluating stock-specific impacts of alternative harvest strategies, using coastal trap net fisheries for Atlantic salmon (*Salmo salar*) in the Baltic Sea as a case study. Our results demonstrate a large variation among stocks in coastal mixed fishery harvest rates, as well as large differences in harvest rates relative to stock-specific maximum sustainable yield (MSY) and recovery levels. Bayesian decision analysis showed that spatio-temporal management actions, such as delayed fishery opening and closed areas may be effective in improving probabilities of meeting management objectives for Baltic salmon. However, stocks did not respond uniformly to different management actions, highlighting the potential for trade-offs in reaching stock-specific targets that must be considered by managers.

Keywords: Atlantic salmon, Bayesian decision analysis, genetic stock identification, mixed-stock fisheries, spatio-temporal management.

Introduction

Simultaneous harvest of multiple populations presents both benefits and challenges for fisheries management and conservation. Yields may be more stable across years because of the buffering effect of inter-population variability in life-history and phenology (i.e. the "*portfolio effect*"; Utter and Ryman 1993; Schindler *et al.*, 2010). On the other hand, mixtures of several populations can sustain high harvest rates on weak populations, leading to overutilization and hampering their recovery (Clayton *et al.*, 1997; Branch *et al.*, 2013). Biocomplexity (i.e. intra-specific genetic variation in life-history traits and phenology) is important for the long-term sustainability of salmon stock complexes and the fisheries that exploit them (Hilborn *et al.*, 2003; Anderson *et al.*, 2008; Schindler *et al.*, 2010).

Fisheries exploiting salmon migrating in the sea or in larger river systems typically catch a mixture of stocks (Koljonen 1995; Boatright *et al.*, 2004; Crozier *et al.*, 2004; Flynn *et al.*, 2006; Koljonen 2006; Vähä *et al.*, 2017), where the contributions of individual stocks are unknown. Quantification of stock-specific exploitation rates can help to avoid the overexploitation and elimination of weak stocks, thus maintaining biocomplexity. For mixed-stock salmon fisheries, quantification of stock-specific exploitation rates typically employs some type of run reconstruction model to allocate catches to stocks (Potter *et al.*, 2004; Branch and Hilborn, 2010). Traditional run reconstruction methods often use information on migration route and timing (Starr and Hilborn 1988; Templin *et al.*, 1996), or age composition data to partition catches among different stocks (e.g. Chasco *et al.*, 2007; Branch and Hilborn 2010). Most recently, a combination of age composition data and genetic stock identification (GSI) has been used to quantify the contributions of different stocks to catches (e.g. Cunningham *et al.*, 2018). The model of Cunningham *et al.*, (2018) extends on earlier approaches (e.g. Branch and Hilborn 2010) by accounting for stock-specific differences in availability to fisheries arising from differences in migratory pathway, accounting for interceptions in terminal fishing areas other than the natal area, and allowing for observation error in catches. Cunningham *et al.*, (2018) utilize information from GSI *via* an observation model for the proportions of different river stocks in catch samples, and account for differences in availability to fisheries by estimating an availability parameter for each stock, area, and year. Below, we extend earlier approaches by using a mechanistic model of migration for multiple Baltic salmon stocks (Whitlock *et al.*, 2018) to describe stock-specific differences in availability, and accounting fully for uncertainty in genetic and catch observations and population dynamics. GSI is integrated into the model, allowing both the genotype data and prior information about stock composition in a given area to inform assignment of sampled individuals to a given stock. Our approach accounts for uncertainty in both stock-of-origin for individual salmon and catches in numbers (*via* observation models), and can be used to predict stock composition in areas/times where no catches or samples have been made.

Naturally reproducing Atlantic salmon (*Salmo salar*, L.) populations persist in less than 30 out of ~100 former salmon rivers (Säisä *et al.*, 2003) in the Baltic Sea. Damming, habitat destruction, pollution, and intensive fishing have been identified as the main causes of population decline (Karlsson and Karlström, 1994; McKinnell and Karlström, 1999; Kuikka *et al.*, 2014). Recent attempts to manage Baltic salmon populations have been partially successful, with the majority of stocks increasing in abundance since the 1990s. However, quantitative assessment (ICES 2018a) indicates large variations in stock status; several stocks have recovered during the last few decades and are now under-exploited relative to the management target, while others are still depleted with a low probability of reaching management objectives and recovery under status quo conditions (ICES, 2018a; Figure 1).

Management context for Atlantic salmon in the Baltic Sea

The International Council for the Exploration of the Sea (ICES) provides annual advice for the management of Baltic salmon in respect of stock size at Maximum Sustainable Yield (MSY). Up to and including 2020, a proxy of 0.75 R_0 (where R_0 is smolt production at the unfished demographic equilibrium) was used for recruitment at MSY. The same proxy was applied to all wild stocks, although analyses indicated differences in the ratio of R_0 to MSY smolt production among stocks (ICES 2018b). Management measures [a total allowable catch (TAC) quota for commercial coastal and offshore fisheries] are currently prescribed and implemented at an aggregate stock level. Under the current management system, this has the implication that if one or a few stocks have not attained their targets within the desired time frame, fishing opportunities may be reduced for all stocks (regardless of their status), since the combined TAC will be affected. In this context, the possibilities to quantify the contributions of wild stocks to catches and evaluate spatio-temporal management actions that can control and alter stock-specific harvest rates are becoming increasingly important, to find fishing scenarios that are compatible with management objectives.

At a national level, the Swedish Agency for Marine and Water Management (hereafter SwAM) has outlined its own management objectives for Baltic salmon. These include reaching at least 0.8 R_0 for wild Swedish stocks by 2025, implementing stock-specific management that makes provisions for weak stocks, full exploitation (targeting) of hatchery-reared salmon by fisheries, and maintaining fisheries that are socially and economically sustainable (HaV, 2015). Similarly, Finland has outlined a national management objective to reach at least 0.8 R_0 with a 25% risk level for its wild salmon stocks by 2020 (Anon. 2015).

Coastal salmon fisheries in the Baltic Sea mainly occur in the northernmost ICES subdivisions 30–31 (Sweden and Finland; Figure 1), where they are currently subject to national TAC quotas in combination with an early season ban, whose duration depends on latitude and management area (ICES subdivision). In Sweden, salmon fishing is currently prohibited until 16th June north of 62 55°N (corresponding roughly to model box 18 and northwards, Figure 1). In Finland, limited fishing during the early summer has been allowed since 2017 for commercial fishers only. Finnish waters in the Gulf of Bothnia are divided into four regulatory zones, over which the opening date is staggered by 5 day intervals. In each zone, fishing season is divided in three periods. The first, early summer period is 39 days long (from May 1st to June 9th in the south-most zone), during which one trapnet per fisher is allowed and up 25% of the individual quota can be utilized. The second period is 7 days (from 10 to 16 June in the south most zone) when two trapnets per fisher are allowed. In the third period, up to four trapnets per fisher are allowed (from 17th June onwards in the south most zone; Finlex, 2017). In 2017, an individual quota system was implemented in Finnish fisheries for salmon, sprat, and Baltic herring.

The continued recovery of productive stocks such as River Torneälven (Finnish name Tornionjoki) on the Finland–Sweden border raises the question of how to set the TAC given large differences in stock status of different rivers, i.e. how to prioritize recovery of weak stocks vs. full exploitation of recovered stocks. The possibility to control exploitation rates on a stock-specific basis, following a stock-specific TAC, would in theory allow the most efficient and sustainable use of this resource. However, up till now, the tools to evaluate stock-specific harvest rates for alternative spatial management actions in mixed fisheries have been lacking.

Bayesian decision analysis provides a rigorous basis for dealing with uncertainty in the provision of fisheries management advice (Walters and Hilborn, 1976; Punt and Hilborn 1997, McAllister and Kirkwood, 1998a, 1998b). A Bayesian decision analytic approach to fisheries stock assessment provides a unified framework for provision of advice to fishery managers in terms of the probabilities of meeting particular objectives or avoiding undesirable outcomes for alternative management actions (Peterman, 2004). In the present study, we perform a Bayesian decision approach to evaluate alternative management actions for the mixed-stock coastal fishery for Baltic salmon, using the 2019 fishing season as an example. As a basis for the analysis, we utilize a modified version of the spatially- and seasonally-structured migration model presented by Whitlock *et al.* (2018), extended to multiple years in a hierarchical framework, and supplemented with catch and effort data for the Swedish and Finnish coastal fisheries.

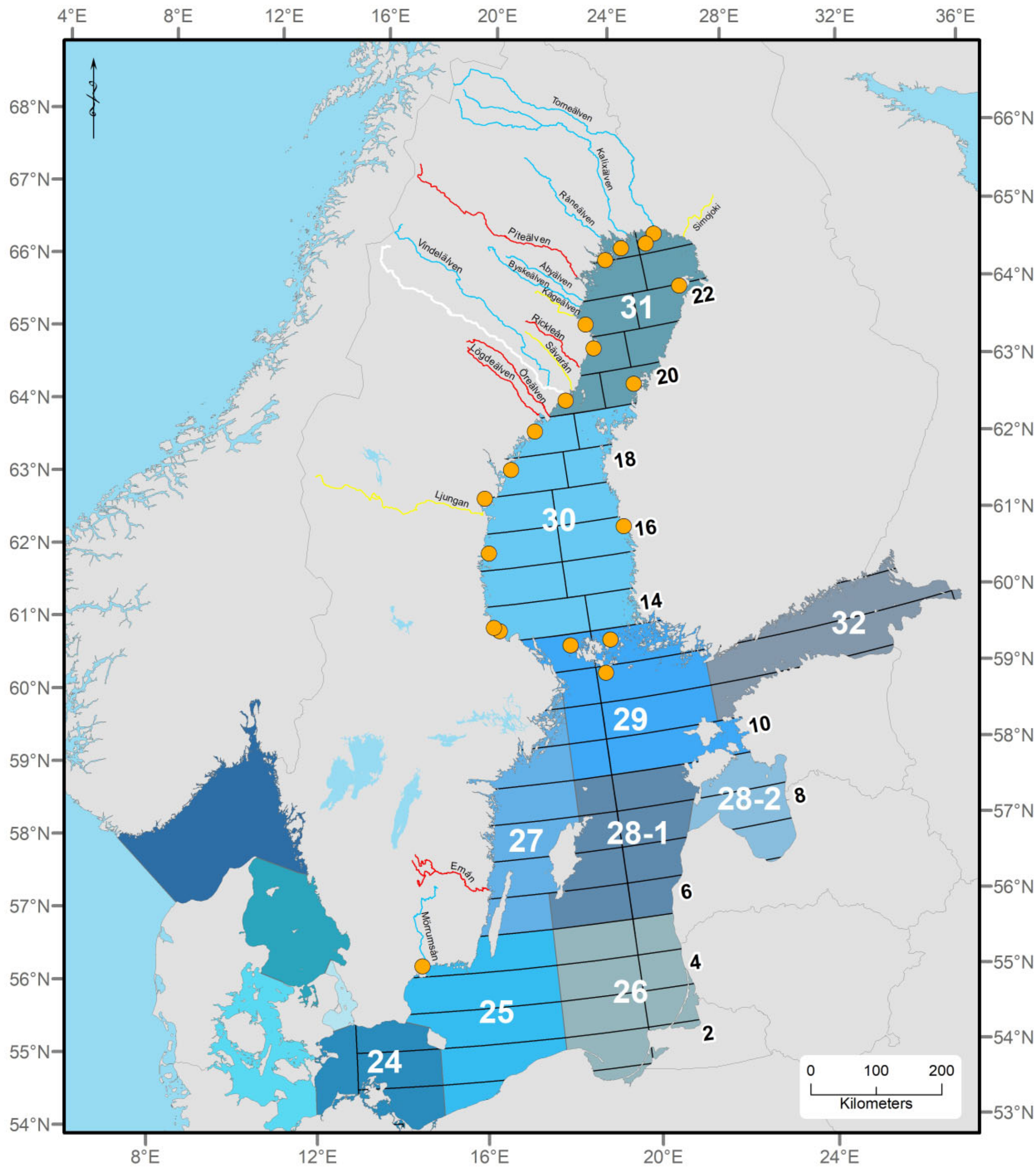

Figure 1. Map of the study area showing model boxes (black grid). Primary (latitudinal) box numbers are shown to the right of the Baltic Sea in black. ICES subdivisions are shaded and numbered in white. Stock status for wild Atlantic salmon stocks in the Baltic Sea according to the 2018 ICES assessment is indicated by the colour of the river (blue, likely or very likely to have reached MSY proxy (75% of unfished equilibrium recruitment); yellow, uncertain; red, unlikely to have reached MSY proxy). The majority of coastal salmon fisheries occur in subdivisions 30 and 31 (Gulf of Bothnia).

Material and methods

A Bayesian decision analysis usually involves the following steps (Punt and Hilborn, 1997):

1) Identifying alternative hypotheses about population dynamics (states of nature, H_i).
2) Determining the relative weight of evidence in support of each alternative hypothesis expressed as a relative probability $P(H_i)$.
3) Identifying alternative management actions A_j.
4) Evaluating the distribution and expected value of each performance measure, I_k, given the management actions and hypotheses.
5) Presenting the results to decision-makers.

Below, we describe the methods followed for steps 1–4 in turn.

Steps 1 and 2: identifying alternative hypotheses about population dynamics and determining the relative weight of evidence in support of each

In the decision analysis for Baltic salmon, alternative hypotheses about states of nature are formulated as prior distributions for population dynamics parameters (natural mortality rates, seasonal movement rates, maturation rates etc.) and states (numbers at age in a given time step and area) in a spatially- and seasonally-structured population dynamics model of the spawning migration of Baltic salmon (the "estimation model"). These prior distributions summarize the degree of belief that each parameter or state takes a particular value before observing any data. The relative weights in support of alternative hypotheses (updated probability that each parameter or state takes a particular value after observing the data) are given by the joint posterior distribution for the population dynamics parameters and states from the estimation model (our application does not include model structural uncertainty). Uncertainty about stock-specific migration timing and route, migration speed, and natural mortality during the coastal migration was incorporated into forward projections by sampling from the joint posterior distribution for these parameters from the estimation model. Uncertainty about the stock-specific abundance of mature salmon on 15th April 2019 (i.e. pre-fishery abundances) was incorporated into the projections by utilizing distributions for abundances on 1st May (summed up over ages) from the 2018 ICES stock assessment (ICES 2018a).

Estimation model

We utilized a modified version of the population dynamics model presented in Whitlock *et al.* (2018), to estimate stock-specific abundances in time and space for 17 wild and 10 hatchery-reared Baltic salmon (*S. salar*) stocks. This model tracks the fortnightly abundances of reproductively mature Baltic salmon in 48 areas, as they migrate north from feeding areas in the Southern Baltic (main basin), along the Swedish and Finnish coasts to their natal rivers for spawning. It spans the coastal fishing period, following the population dynamics of migrating mature salmon between April 15th and August 18th in each year. An observation model for microsatellite allele frequency data at 17 loci, sampled at multiple locations over the fishing season is used together with a genetic baseline to learn about stock composition in time and space. Modifications to the model in Whitlock *et al.* (2018) comprise a more flexible description of movement around the natal river, and extension to a hierarchical structure for migration start dates and the initial spatial distribution to accommodate multiple years of data. We also add observation models for the total catch in numbers in the Swedish and Finnish coastal fisheries in 2013 and 2014, as well as the proportion of the catch that is comprised of wild salmon based on fin-clipping data (Swedish catches only). This addition allows estimation of stock-specific catches in the coastal fishery, based on the underlying estimated stock composition in each time-area stratum. The estimation model, including the new modifications, is described in detail in Appendix A of the Supplementary Material.

Data

The baseline used in this study includes information on 17 DNA microsatellite loci for individuals originating from 27 rivers, of which 17 support naturally reproducing (wild) salmon stocks and ten are hatchery-reared stocks. The river stocks span from the River Torneälven in the north to River Mörrumsån in the south (Figure 1). Further details can be found in the Supplementary Material.

The stock mixture data comprise 1884 adult individuals sampled from coastal trap nets at 14 locations along the Swedish and Finnish coasts between 28th May and 10th August in 2013, and 2058 adult individuals sampled between 5th May and 11th August in 2014 (Östergren *et al.*, 2015). In addition to scale samples for DNA microsatellite analysis (17 loci), we obtained individual data on catch date, location, and adipose fin status (present/absent). Hatcheries in Sweden routinely remove the adipose fin from hatchery-reared salmon smolts released into exploited rivers, providing a further means to distinguish between wild and reared stocks. Alleles found in a mixture sample, but not in the baseline, were excluded from analyses as in Bolker *et al.* (2007). Samples from traps located in the same model box were combined for purposes of statistical analysis.

Catch and effort data for the years 2013 and 2014 were added to the estimation model as an extension of the model described in Whitlock *et al.* (2018). The catch data for the Swedish coastal fishery were provided by SwAM, and comprise the number of salmon taken with type (wild or reared; all hatchery reared individuals have their adipose fin removed), date, latitude, and longitude, as well as effort data on the number of trap net days. Similar data were obtained for the Finnish trap net fishery from Natural Resources Institute Finland (Luke), although landings were not identified to wild or reared origin (according to fin-clipping) in the Finnish log book data. Catch and effort data were summed into 2-week time steps in each year, from the 15th April to the 18th August and into half-degree latitude boxes for the eastern and western Baltic Sea (Figure 1).

Step 3: identifying alternative management actions

We use forward projections of population dynamics (assuming the same dynamics as in the estimation model), but with catches defined by alternative spatio-temporal fishing effort configurations that form the candidate management actions. We evaluate four alternative management actions for the coastal trap net fishery in 2019, based on re-allocation of the totals of reported fishing effort in 2018, in Sweden and Finland, respectively. The four management options are as follows:

1) Status quo distribution of fishing effort (same as in 2018). Regional quotas are applied by ICES subdivision (Figure 1) in Sweden following SwAM regulations for 2018 (200, 7500, and 19000 salmon for subdivisions 22–29, 30, and 31, respectively). In addition, among the 19000 salmon allowed to be landed in subdivision 31, a maximum of 12000 can be of wild origin (identified by intact adipose fin). Once this quota on wild salmon is filled, only reared (fin-clipped) salmon can be retained and an incidental mortality rate of 11% is applied for wild salmon that are released (Siira *et al.*, 2006). In Finland, the national TAC for all ICES subdivisions combined is applied.
2) Fishing effort is set equal to zero outside six wild rivers (all Swedish) with poor status (less than 30% probability to reach 0.75 R_0 in 2017: Emån, Lögdeälven, Öreälven, Piteälven, Rickleån, and Testeboån (Figure 2)), as estimated in the 2018 ICES stock assessment (ICES 2018a). We assume that fishing effort is removed and not displaced to other areas; the quota is not affected. National TACs (2018 regulations) of 26700 (Sweden) and 23548 (Finland) salmon are applied, and effort is set to zero once the quota is exceeded.

Figure 2. Map showing closed areas (diagonal hatching) outside rivers of poor stock status as estimated in the 2018 stock assessment for the closed areas management option.

3) Removal of the early season fishing ban. On the Swedish side, effort is unchanged up to 62 55°N (approximately the southern boundary of box 18, Figure 1). North of 62 55°N, where an early season ban currently applies, effort is set equal to the maximum observed fortnightly effort in 2018 from the end of May up to the fortnight of maximum effort, and the observed effort thereafter (gradual decrease of fishing effort towards the end of the season).

On the Finnish side, effort is set equal to the maximum observed effort in 2018 from the end of April up to the fortnight of maximum effort in ICES subdivisions 29–30. In ICES subdivision 31, effort is set equal to the maximum observed effort in 2018 from the end of May up to the fortnight of the maximum observed effort in ICES subdivision 31. After this, the effort is set equal to the observed 2018 effort in all subdivisions. National TACs of

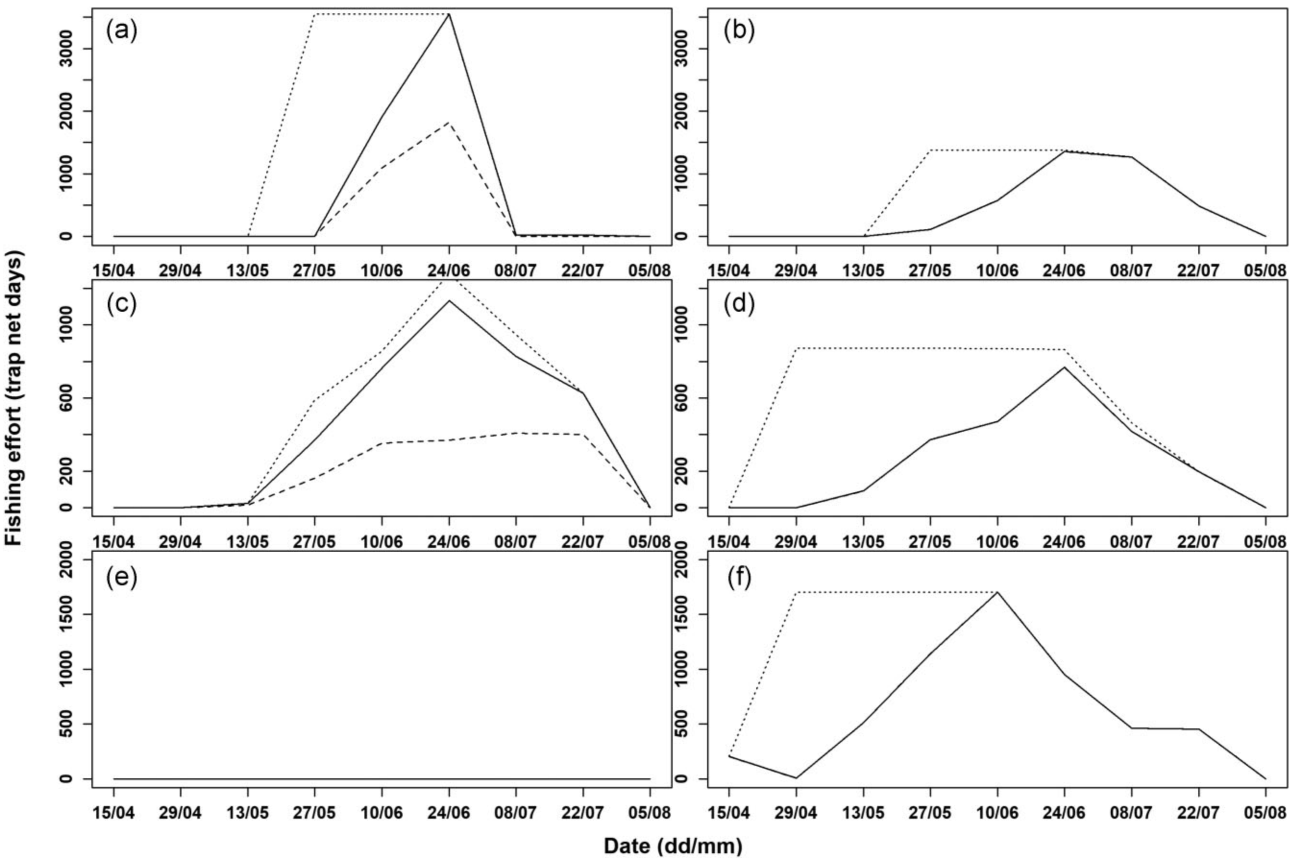

Figure 3. Fishing effort configurations for alternative management options. Solid line, status quo, and retention ban options; dotted line, early season fishing option; dashed line closed areas option. (a) ICES subdivision 31, Swedish side; (b) ICES subdivision 31, Finnish side; (c) ICES subdivision 30, Swedish side; (d) ICES subdivision 30, Finnish side; (e) ICES subdivision 22–29, Swedish side; and (f) ICES subdivision 22–29, Finnish side.

26700 (Sweden) and 23548 (Finland) salmon are applied (2018 regulations), and effort is set to zero once the quota is exceeded.

4) Retention ban for wild salmon (identified by an intact adipose fin) until 24th June. We assume a post-release mortality rate of 11% for wild salmon (Siira *et al.*, 2006). Fishing effort is assumed to be the same as in 2018. National TACs of 26700 (Sweden) and 23548 (Finland) salmon are applied (2018 regulations), and effort is set to zero once the quota is exceeded.

Note that the closed areas and early season fishing options represent a change in the overall level of fishing effort (a reduction of 28% and increase of 56%, respectively). A graphical representation of the effort by ICES subdivision for the different management options in the Finnish and Swedish coastal fisheries is provided in Figure 3. In the text that follows, the four options above are referred to as "status quo," "closed areas," "early season fishing", and "retention ban."

Data

Fishing effort data for 2018 are used in the projections model. These data were provided in the same format as those for 2013 and 2014. Effort data were summed into 2-week time steps in each year, from the 15th April to the 18th August and into half-degree latitude boxes for the eastern and western Baltic Sea (Figure 1), to provide the status quo scenario on which other management options are based.

Step 4: evaluating the distribution and expected value of performance measures

To illustrate our approach, we chose to look at four performance measures in 2019:

i) The probability that the harvest rate that maximizes the long term yield (HR^{MSY}) is exceeded, evaluated for each wild river stock.

ii) Total catch (wild and reared combined).

iii) The proportion of the total catch comprised by reared stocks.

iv) The probability that the harvest rate giving at least 70% chance of recovery (60% for Emån, see below) to B^{MSY} within two generation times (a commonly used timeframe for recovery e.g. Marine Stewardship Council, 2014), HR^{rec}, is exceeded. This recovery harvest rate will be lower than the MSY harvest rate for stocks that have not reached MSY. We assume two generation times to be equivalent to 10 years (e.g. Mäkinen *et al.*, 2015).

We chose to include performance measure iv) since implementation of HR^{MSY} implies recovery of overfished wild stocks towards biomass at MSY (B^{MSY}), but with an unspecified timeframe that may not be compatible with management objectives.

Calculations for stock-specific and total catches in the decision analysis (projections model) can be found in Appendix B of the Supplementary Material.

Calculation of stock specific management targets

As an alternative to the 0.75 R_0 proxy for MSY recruitment used by ICES, we evaluated HR^{MSY} and HR^{rec} for each wild salmon stock in the estimation model, using an age-structured full life-cycle model (a modified version of the future fishing scenarios used to provide advice within ICES). Mörrumsån and Emån were omitted from this analysis, since they are assumed to experience zero coastal fishery harvest in the ICES assessment model. Testeboån was also omitted as it was not included in ICES's assessment at the time of analysis. The ICES stock projections are used to evaluate probabilities of reaching management targets in each future year, for different levels of future fishing effort. They use the joint posterior distribution from the ICES assessment model for fishery related and population dynamics parameters and abundances at age. All salmon are assumed to die after spawning, and a Beverton–Holt stock-recruit function describes the relationship between stock-specific egg production and the number of smolts. The projections incorporate process errors in annual stock–recruit deviations, rates of post-smolt mortality, maturation rates, and M74 egg mortality. Future removals by offshore longline (immature salmon) and coastal trapnet fisheries (mature salmon) are modelled using harvest rates calculated as a product of catchabilities from the assessment model and input fishing effort levels. In the ICES assessment model, (recreational) river harvest rates are assumed to be the same for all wild stocks, and the posterior distribution for the river harvest rates are used in the projections. In stock projections, these river harvest rates remain the same across all candidate effort (fishing mortality levels), and similarly, prior to 2021, the recreational trolling catch at sea was assumed to be the same in all fishing mortality scenarios (because these are not currently included in the catch quota). However, in this exercise, it was found that some stocks never reach a 70% probability of recovery to MSY spawner escapement in the specified time-frame (presumably because the harvest from recreational fisheries alone is too high). We therefore allow both river and recreational trolling catches to be reduced by the same proportion as commercial catches in calculations of HR^{MSY} and HR^{rec}.

Stock-specific estimates of HR^{MSY} and spawner escapement at MSY (S^{MSY}) were obtained using optimization (with the *optimize* function in R), where future population dynamics were simulated under different effort levels, and the average long-term yield (summed over ages and fisheries) was calculated assuming that the current pattern of relative fishing effort among different fisheries will continue in the future. This is one of many possible assumptions about the development of fishing effort, and it should be noted that alternative assumptions will likely lead to different estimates of MSY harvest rates in the coastal fishery. Harvest rates corresponding to a 70% chance of recovery within two generation times were obtained in a second round of optimization to find the harvest rates corresponding to a 70% probability of reaching S^{MSY} within 10 years.

The population dynamics in the ICES stock projections, including calculation of harvest rates and spawner numbers for MSY analyses are described in Appendix C of the Supplementary Material.

Results

In this section, we present results from the estimation model with genetic and catch data for the years 2013 and 2014. These are followed by results from the stock projections for 2019 (Bayesian decision analysis).

Table 1. Median estimates of the harvest rate at maximum sustainable yield (MSY) and harvest rates associated with a $>=$ 70% probability of reaching MSY escapement within 10 years (Recovery harvest rate). Stock status: U (unlikely), <30% probability of reaching 75% of smolt production capacity in 2017; I (intermediate), 30–69% probability of reaching 75% of smolt production capacity in 2017; and L (likely), $>=$ 70% probability of reaching 75% of smolt production capacity in 2017.

Stock	Status (ICES 2018a)	MSY harvest rate (year^{-1})	Recovery harvest rate (year^{-1})	Ratio
Simojoki	I	0.15	0.08	0.53
Torneälven	L	0.24	0.16	0.67
Kalixälven	L	0.33	0.24	0.73
Råneälven	L	0.24	0.16	0.67
Piteälven	U	0.20	0.13	0.65
Åbyälven	L	0.18	0.11	0.60
Byskeälven	L	0.23	0.17	0.73
Kågeälven	I	0.17	0.08	0.48
Rickleån	U	0.16	0.07	0.45
Sävarån	I	0.16	0.08	0.51
Vindelälven	L	0.18	0.11	0.61
Öreälven	U	0.16	0.05	0.32
Lögdeälven	U	0.14	0.01	0.07
Ljungan	I	0.17	0.10	0.60

Harvest rates

Median estimates of harvest rate at MSY in the coastal trap net fishery for Baltic salmon ranged from 0.13 year^{-1} (Lögdeälven stock) to 0.33 year^{-1} (Kalixälven stock; Table 1). Per definition, recovery harvest rates were lower than MSY harvest rates, but their ratio varied among stocks (Table 1). Estimated harvest rate reference points tended to be higher for stocks with good status according to 2018's assessment (Table 1).

Estimated stock-specific catches and harvest rates showed large variation among stocks (Figure 4). The Torneälven and Kalixälven stocks (in the northern Bothnian Bay) together were estimated to account for ∼70–80% of catches of wild salmon in 2013 and 2014. Harvest rates in the coastal fishery varied between ∼0.1 and 0.5 year^{-1} for wild Baltic salmon stocks, with the exception of Mörrumsån and Emån (Southern Sweden), which are not encountered in the coastal trap net fishery in Gulf of Bothnia (Figure 4). Estimated harvest rates in the coastal fishery were generally either greater than both HR^{MSY} and HR^{rec}, or intermediate between these two quantities, with the exceptions of Torneälven and Piteälven in 2013 and Vindelälven in 2014, where harvest rates were below HR^{rec}. In 2013, ten rivers out of 14 had posterior median harvest rates less than HR^{MSY}, while four had posterior median harvest rates greater than HR^{MSY}. In 2014, five wild stocks had posterior median harvest rates less than HR^{MSY}, while nine had posterior median harvest rates greater than HR^{MSY} (Figure 4).

Migration patterns

Extending the model to a hierarchical structure allowed estimation of migration start time in the Southern Baltic Sea for each stock (Figure 5). Estimated migration start dates were earlier in 2014 compared to 2013, while wild stocks were generally estimated to start migrating earlier than reared stocks in both years.

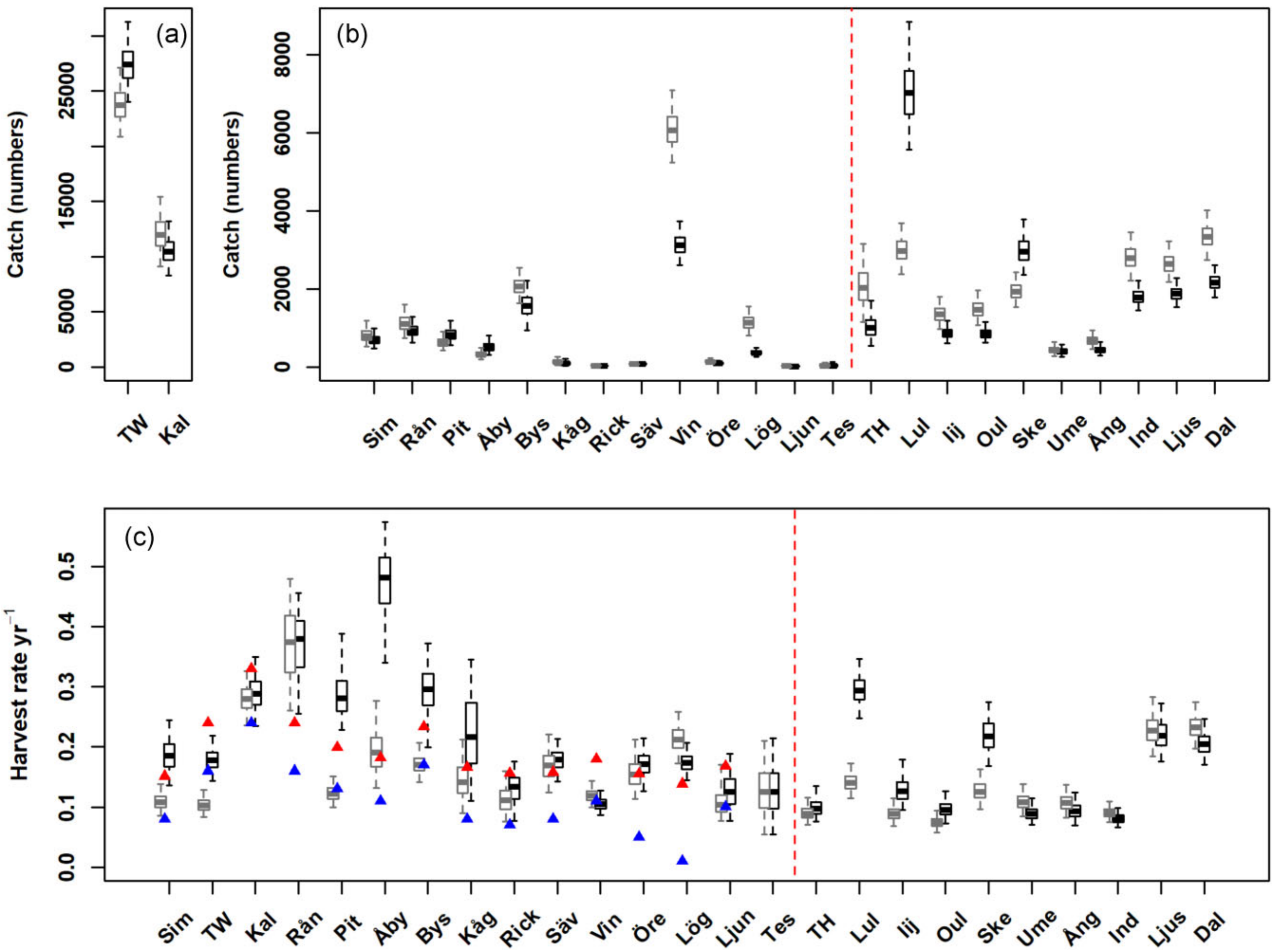

Figure 4. Estimated stock-specific catches for the Torneälven wild and Kalixälven stocks (a) and other Baltic salmon stocks (b) in 2013 (grey boxes) and 2014 (black boxes). (c) Estimated coastal fishery harvest rates in 2013 and 2014. Red symbols indicate median estimates of the MSY harvest rate. Blue symbols indicate median estimates of the recovery harvest rate. Stocks to the left of the dashed vertical line are wild, while those to the right are reared. Grey boxes, 2013; black boxes, 2014. Horizontal lines within each box indicate posterior medians, whilst the boxes indicate 50% posterior probability intervals. Whiskers denote the 95% posterior probability interval. Stock abbreviations: "Sim," Simojoki; "TW," Torne wild; "Kal," Kalixälven; "Rån," Råneälven; "Pit," Piteälven; "Åby," Åbyälven; "Bys," Byskeälven; "Kåg," Kågeälven; "Rick," Rickleån; "Säv," Sävarån; "Vin," Vindelälven; "Öre," Öreälven; "Lög," Lögdeälven; "Ljun," Ljungan; "Tes," Testeboån; "TH," Torne hatchery; "Lul," Luleälven, "Iij," Iijoki; "Oul," Oulujoki; "Ske," "Skellefteälven"; "Ume," Umeälven; "Ång," Ångermanälven; "Ind," Indalsälven; "Ljus," Ljusnan; and "Dal," Dalälven.

Catches

The model provided a fairly good fit to the observed catch data (Figure 6). Catches in ICES subdivision 31 were highest during the fortnight 24th June–8th July. Spatially, catches reflected the progressive northwards migration of salmon, with higher catches (relative to the maximum in a given area) in early June at lower latitudes and during July at higher latitudes.

Bayesian decision analysis

Of the four management measures evaluated for 2019, the mean proportion of reared salmon in the catch was highest under the retention ban option, with a ban on landing wild salmon until 24th June (Table 2). Closed areas outside six weak wild Swedish rivers (Figure 2) and early season fishing led to lower proportions of reared fish in the catch than under the status quo. The lower proportion of reared salmon in the catch under the closed areas option could result from a number of factors. The northernmost closed area (Figure 2) likely results in reduced catches for the Luleälven reared stock, which accounts for the highest estimated catch among reared stocks (Figure 4b). In addition, reared stocks contributing most to catches (Luleälven, Skellefteälven) were estimated to migrate closer to the Swedish coast, thus benefitting from the closures, in contrast to wild stocks contributing most to catches overall (Torneälven, Kalixälven; Figure 4a).

Total catch (wild and reared salmon) was highest under the early season fishing option and lowest under the closed areas management option (Table 2). For wild salmon, total catch was highest under the early season fishing option and lowest under the retention ban management option (Table 2). In Sweden, the national TAC was not fully utilized under the closed areas and retention ban management options, while in Finland in was underutilized in the retention ban option. Total catches for both countries came close to the national TACs under the status quo management option. Note that realized catches can exceed the TAC in our projections, since effort was set equal to zero from the first 2-week time step when the total catch was greater than the TAC. The distribution of catches among

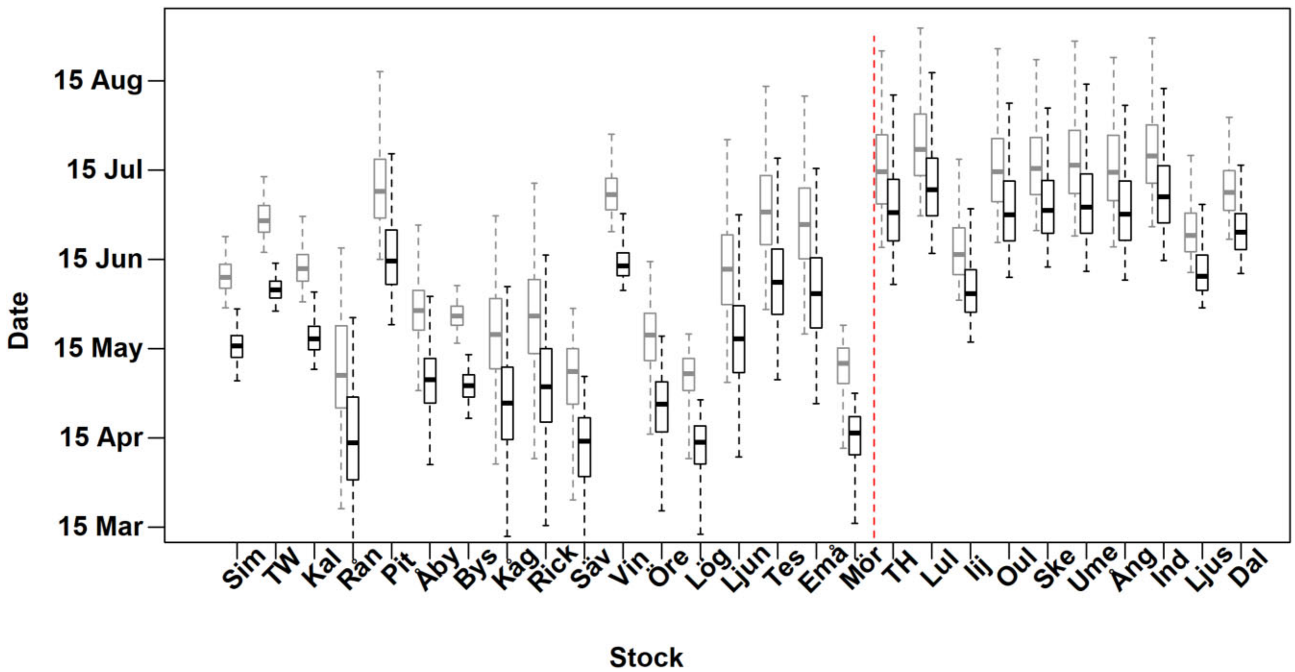

Figure 5. Posterior distributions for estimated migration start dates in the estimation model for individual Atlantic salmon salmon river stocks in the Baltic Sea. Stocks to the left of the dashed vertical line are wild, while those to the right are reared. Grey boxes, 2013; black boxes, 2014. Horizontal lines within each box indicate posterior medians, whilst the boxes indicate 50% posterior probability intervals. Whiskers denote the 95% posterior probability interval. Stock abbreviations: “Sim,” Simojoki; “TW,” Torne wild; “Kal,” Kalixälven; “Rån,” Råneälven; “Pit,” Piteälven; “Åby,” Åbyälven; “Bys,” Byskeälven; “Kåg,” Kågeälven; “Rick,” Rickleån; “Säv,” Sävarån; “Vin,” Vindelälven; “Öre,” Öreälven; “Lög,” Lögdeälven; “Ljun,” Ljungan; “Tes,” Testeboån; “TH,” Torne hatchery; “Lul,” Luleälven, “Iij,” Iijoki; “Oul,” Oulujoki; “Ske,” “Skellefteälven”; “Ume,” Umeälven; “Ång,” Ångermanälven; “Ind,” Indalsälven; “Ljus,” Ljusnan; and “Dal,” Dalälven.

the nation states differed according to the management action: under the closed areas option, the Finnish catch share was estimated to increase, while Swedish catches decreased relative to the status quo (Table 2). Under the retention ban management option, the Swedish share of the total catch was higher relative to the status quo (Table 2).

Under status quo management of the coastal fishery, there was a fairly large variation among stocks in the probability to exceed the MSY harvest rate. A total of two stocks (Råneälven and Åbyälven) had a probability greater than 0.50 to exceed the MSY harvest rate (Table 3, Supplementary Figure S1; both of these stocks have good status according to the 2018 assessment). Among the poor status stocks, probabilities to exceed the MSY harvest rate in the coastal fishery were low (maximum 0.20). Closing areas outside poor status rivers and a retention ban on wild salmon were both effective in reducing the probability to exceed the MSY harvest rates, although stock-specific effects varied (Table 3, Supplementary Figures S2 and S4). For example, the Simojoki stock did not show a reduction in the probability to exceed HR^{MSY} under the closed areas option, possibly because of migration primarily along the Finnish coast. For the two stocks with a > 50% probability to exceed HR^{MSY} under the status quo, one stock (Åbyälven) showed a greater reduction in risk for the closed areas option, and the other (Råneälven) under the retention ban option. Removal of the early season fishing ban led to an elevated probability to exceed HR^{MSY} for all stocks relative to the status quo, with four of the 14 stocks having a probability > 50% to exceed HR^{MSY}, including two poor or intermediate status stocks (Table 3, Supplementary Figure S3).

Probabilities to exceed the recovery harvest rate, HR^{rec} were much higher than stock-specific probabilities to exceed HR^{MSY}, with eight of the 14 stocks projected to have a > 50% probability to exceed HR^{rec} under the status quo (Table 3, Supplementary Figure S1). Closing areas outside rivers with poor stock status to fishing, and a retention ban on wild salmon in the early fishing season both led to a reduced probability to exceed HR^{rec}, with four (including two poor status stocks) stocks having a > 50% probability to exceed HR^{rec} under the closed areas option, and four stocks (including two poor status stocks) under the retention ban option (Table 3; Supplementary Figures S2 and S4). Under the early season fishing management option, only five out of 14 stocks had probabilities to exceed $HR^{rec} \leq 50\%$, including one out of four weak stocks (Table 3). In summary, under status quo management, harvest rates may not be consistent with the recovery of wild stocks that are below B^{MSY} within two generation times. Establishing no-take areas or a ban on retention on wild fish could aid the recovery of wild stocks, while removal of the early season ban is expected to slow the recovery of weak wild stocks.

Discussion

Management of mixed-stock systems with potentially diverse stock status presents a challenge for fisheries scientists and managers. GSI methods have the potential to improve estimation of stock-specific harvest rates (Cadrin *et al.*, 2005; Branch and Hilborn 2010) and stock productivities (e.g. Cunningham *et al.*, 2018) in a mixed-stock setting. We integrated GSI into a spatially structured model for migrating salmon stocks interacting in a mixed fishery to estimate stock-specific harvest rates, and evaluate alternative management actions using Bayesian decision analysis. Our new approach can help to clarify trade-offs among stocks in accomplishing management objectives. It extends earlier work on run reconstruction

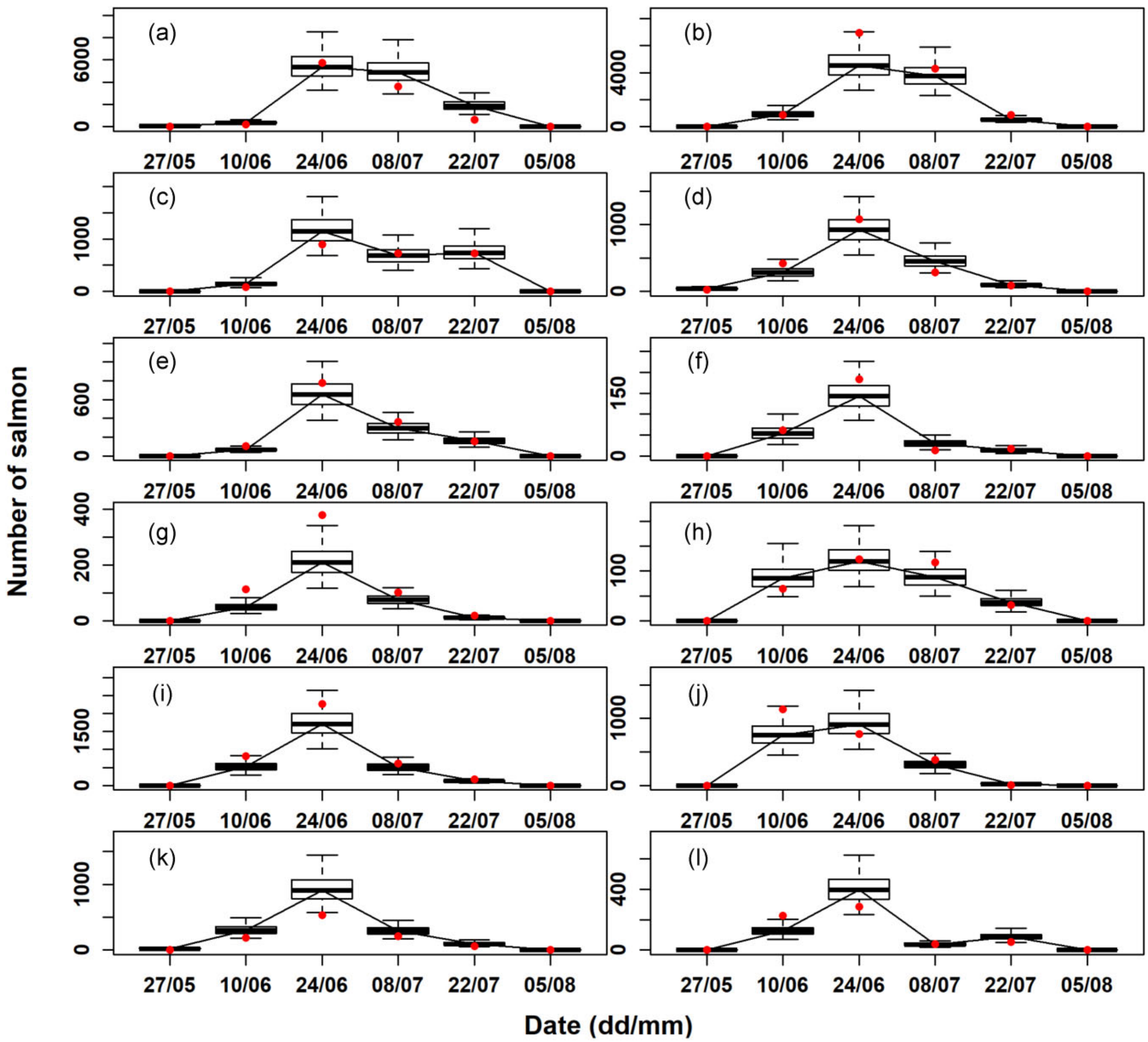

Figure 6. Posterior predictive distributions for Atlantic salmon catches in the Baltic Sea in 2013. Left column, western Gulf of Bothnia; right column, eastern Gulf of Bothnia. (a) and (b) Model box 24; (c) and (d) model box 23; (e) and (f) model box 22; (g) and (h) model box 21; (i) and (j) model box 20; and (k) and (l) model box 19. Red symbols denote observed catches. Horizontal lines within each box indicate posterior medians, whilst the boxes indicate 50% posterior probability intervals. Whiskers denote the 95% posterior probability interval. Note that the *y*-axis scale differs between boxes.

Table 2. Mean proportion of reared salmon in catches and mean catches (in numbers, all stocks combined) with 90% probability interval in parentheses, for different management actions in 2019.

Performance measure	Status quo	Closed Areas	Early season fishing	Retention ban
Proportion reared in catch	0.29 (0.16–0.47)	0.21 (0.10–0.39)	0.25 (0.08–0.49)	0.40 (0.24–0.60)
Total catch wild salmon	33 527 (16 567–55 049)	31 544 (14 594–56 930)	42 680 (20 527–72 263)	22 054 (10 467–44 786)
Total escapement wild salmon	158 198 (71 711–319 819)	161 488 (73 393–327 626)	143 374 (66 379–287 292)	168 017 (74 556–341 593)
Total catch Sweden (TAC 26700)	26 405 (12 946–43 597)	17 166 (7 745–35 050)	29 315 (14 780–48 782)	23 825 (10 901–46 333)
Total catch Finland (TAC 23548)	22 776 (11 302–32 938)	24 031 (11 338–32 942)	26 938 (16 170–43 304)	15 030 (6 853–28 121)
Total catch Sweden and Finland	49 438 (24 988–74 681)	41 729 (19 541–67 230)	57 869 (31 423–86 278)	38 999 (17 920–73 451)

Table 3. Probabilities that stock-specific MSY and recovery harvest rates are exceeded for 14 wild Baltic salmon stocks in the 2019 fishery under different management actions. Stock status (assessed for 2017): U, <30% probability of reaching 75% of smolt production capacity; I, 30–69% probability of reaching 75% of smolt production capacity; and L, > = 70% probability of reaching 75% of smolt production capacity.

		Probability MSY harvest rate exceeded				Probability recovery harvest rate exceeded			
Stock	Status (ICES 2018a)	Status quo	Closed areas	Early season fishing	Retention ban	Status quo	Closed areas	Early season fishing	Retention ban
Simojoki	I	0.05	0.06	0.37	0.00	0.69	0.70	0.82	0.17
Torneälven	L	0.00	0.00	0.01	0.00	0.01	0.01	0.07	0.00
Kalixälven	L	0.07	0.03	0.22	0.00	0.35	0.29	0.59	0.05
Råneälven	L	0.80	0.79	0.93	0.43	0.97	0.97	0.98	0.90
Piteälven	U	0.09	0.00	0.16	0.02	0.40	0.00	0.48	0.18
Åbyälven	L	0.75	0.00	0.87	0.45	0.97	0.03	0.99	0.95
Byskeälven	L	0.00	0.00	0.07	0.00	0.04	0.00	0.39	0.00
Kågeälven	I	0.09	0.00	0.42	0.00	0.74	0.31	0.92	0.27
Rickleån	U	0.00	0.00	0.23	0.00	0.73	0.35	0.90	0.00
Sävarån	I	0.02	0.00	0.69	0.00	0.92	0.36	0.99	0.01
Vindelälven	L	0.00	0.00	0.01	0.00	0.04	0.00	0.16	0.00
Öreälven	U	0.01	0.00	0.49	0.00	0.99	0.89	1.00	0.67
Lögdeälven	U	0.20	0.00	0.85	0.00	1.00	1.00	1.00	1.00
Ljungan	I	0.00	0.00	0.05	0.00	0.27	0.29	0.39	0.00

models by accounting for uncertainty in population dynamics parameters (e.g. rates of movement and natural mortality), in addition to uncertainty associated with genetic assignments and catches. This is an important step for evaluating the risk associated with different management actions in a decision analysis. Integrating mixed-stock analysis into a mechanistic model of migration also allows predictions of stock composition to be made for areas or times from which no catch samples are available.

Performance of management options in relation to objectives

Our results reveal that while harvest rates in the coastal fishery for Baltic salmon have a relatively low probability of exceeding the MSY harvest rate for most wild stocks, current harvest rates are inconsistent with the recovery of poor-status stocks over the time frame examined (two generations or ca. 10 years). Closing areas outside rivers with poor stock status (for all or part of the fishing season), and restrictions on retention of wild salmon may have potential for implementing recovery goals based on our results.

Among the management options evaluated in our study, the retention ban on wild salmon performed the best in terms of yielding the highest proportion of reared fish in the catch, although this option also resulted in the greatest reduction in total catch. It performed comparably to the closed areas option in terms of lowering the risk of exceeding the recovery harvest rate (HR^{rec}). For the retention ban option, we assumed a release mortality rate of 11%, based on the results of Siira *et al.* (2006). However, ongoing studies investigating survival of released salmon from pontoon traps, which is the most commonly used gear in the coastal fishery for salmon, indicate a higher release mortality rate (Östergren *et al.,* in press). Furthermore, we assumed 100% compliance with regulations in our study, although in reality it is unknown, how closely fishermen might follow rules concerning release of wild fish. Our evaluations of the impact of a retention ban might thus be on the optimistic side in terms of mortality rates for wild salmon.

The option of closed fishing areas outside the weak wild rivers decreased the proportion of reared fish in catches as well as decreasing the total catch. In our study, the closed areas were quite large, so it is understandable that they limited reared fish catches as well. The size and location of closed areas at the river mouths could, however, be varied and this type of management action may still be useful in some cases, especially if all reared fish are not marked.

Given the pronounced variation in status among wild Baltic salmon stocks, the use of a single TAC to regulate the coastal mixed-stock fishery (ICES subdivisions 22–31) may not be consistent with achieving management objectives over a short-medium term time frame. Attempts to steer exploitation towards reared salmon and reduce exploitation on weak wild stocks, by splitting the national quota into regional quotas, have been made in Sweden during the last few years (our status quo option) with variable success (e.g. ICES 2019). However, our results show that additional management regulations could improve probabilities to meet such national management objectives. Achieving a high probability of recovery to MSY abundance within 10 years for all stocks was shown to be challenging given the managmenet actions evaluated, but combining them in some form could yield better outcomes. Moreover, our results indicate that in order to move towards MSY spawner abundance over two generations, comparable reductions in fishing effort would likely be needed in other fisheries exploiting Baltic salmon, including recreational fisheries at sea and in rivers that are not currently subject to quota regulations.

Starting from 2021, stock-specific smolt production at MSY is used by ICES to assess stock status, together with limit smolt production (defined as the minimum smolt production that results in MSY smolt production in one generation time, ICES 2020). This has been accompanied by a new goal of achieving limit smolt production for all stocks over a shorter time frame than used in this study. In this context, the ability to evaluate spatio-temporal management actions for mixed fisheries that can protect weak stocks and continue to exploit healthy ones is more relevant than ever.

Owing to the somewhat complex stock-specific spatio-temporal patterns of migration in Baltic salmon, management actions can have unanticipated consequences. One of the benefits of our approach is that (sometimes unexpected) trade-offs are made explicit, and can thus be weighed up by managers. For example, the closed areas management option resulted in diminished Swedish catches and slightly increased Finnish catches relative to the status quo. While the decrease in Swedish catches is expected, given the locations of closed areas along the Swedish coast, the increased Finnish catch likely results from higher survivorship of salmon (mainly from the Torne River and Kalixälven stocks) migrating through closed areas in Swedish waters that precede the major Finnish fisheries in the northern Bothnian Bay. In contrast, under the retention ban management option, there was a greater relative decrease in Finnish catches compared with the status quo. This likely reflects the higher proportion of wild origin stocks migrating along the Finnish coast compared with the Swedish coast, so that catches in Swedish waters would be affected to a lesser degree by a release regulation on wild salmon.

The estimated difference between migration start dates in 2013 and 2014 (later in 2013) is in agreement with previous observations on variation in sea surface temperature and arrival dates of migrating salmon at the coast; following cold winters (2013 was colder than 2014); salmon tend to arrive later to the coast and *vice versa* (Karlsson *et al.*, 1995). Our finding of earlier estimated migration start dates for wild salmon stocks compared with reared ones is also consistent with earlier studies (e.g. McKinnell *et al.*, 1994). Migration timing estimates could potentially be improved by adding additional years of genetic data to the model. In particular, information on fin-clipped salmon in Finnish coastal catches could be included in future analyses, since fin-clipping of reared smolts recently became mandatory in Finland. The model could also be extended to incorporate data on age composition data as well as genetic information to apportion catches (e.g. Cunningham *et al.*, 2018). In the Baltic, stocks from more northern rivers tend to smoltify at older ages than southern ones, and wild stocks at older ages than reared ones. This information could help to reduce uncertainty in stock assignments as well as improving estimates of migration timing in an age-structured model. In this study, we have evaluated different types of spatio-temporal management actions, but we did not consider an individual quota system (as adopted in Finland since 2017). This would require adding a description of individual fisher behaviour to the model, and would be a further avenue for future research.

Although, the alternative management options evaluated in this study are somewhat arbitrary and may not be realistic to implement in their entirety, our results demonstrate the utility of the approach to evaluate a wide variety of management options/scenarios aimed at reducing exploitation rates on weak stocks and/or increasing exploitation on reared stocks in the coastal mixed-stock fishery for Baltic salmon. The model presented above can also be used to evaluate the effects of different management options on total catches and catch distribution between nations.

We have developed a framework for the apportionment of catches among stocks and evaluation of alternative management actions for mixed-stock fisheries that accounts for uncertainty in stock-specific migration dynamics, as well as observation error associated with catches and genetic data. Stock-specific harvest rate estimates for the coastal fishery generated by our approach can be used to improve the description of this fishery in the stock assessment for Baltic salmon (ICES 2019), where it is currently assumed that groups of wild and reared stocks (so-called assessment units) share the same coastal fishery harvest rate. This should increase the accuracy of stock-specific status evaluations as well as allowing evaluation of spatial and temporal management actions for mixed fisheries. Such approaches can make clear trade-offs in terms of expected effects of management actions on different stocks and fishery yields, and support development of management actions that are consistent with stock-specific targets at both international and national levels.

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Supplementary data

Supplementary material is available at the *ICESJMS* online version of the manuscript.

Author contributions

J.D., S.P. T.P., and R.W. conceived and developed ideas; J.Ö. organized collection and analysis of scales in Sweden; T.P. assembled Finnish catch and genetic data; M.-L.K. maintained the Baltic Atlantic salmon microsatellite DNA baseline; R.W. developed the population dynamics model and performed Bayesian decision analyses for Baltic Atlantic salmon; and R.W. led writing of the manuscript and all authors contributed to the drafts and gave final approval for publication.

Data availability statement

Data have been deposited in the Dryad Digital Repository https://doi.org/10.5061/dryad.4pg37 (Whitlock *et al.*, 2018).

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