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Integrated, age-structured, length-based stock assessment model with uncertain process variances, structural uncertainty, and environmental covariates: case of Central Baltic herring

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Abstract: We developed a generic, age-structured, state-space stock assessment model that can be used as a platform for including information elicited from stakeholders. The model tracks the mean size-at-age and then uses it to explain rates of natural and fishing mortality. The fishery selectivity is divided to two components, which makes it possible to model the active seeking of the fleet for certain sizes of fish, as well as the selectivity of the gear itself. The model can account for uncertainties that are not currently accounted for in state-of-the-art models for integrated assessments: (*i*) The form of the stock–recruitment function is considered uncertain and is accounted for by using Bayesian model averaging. (*ii*) In addition to recruitment variation, process variation in natural mortality, growth parameters, and fishing mortality can also be treated as uncertain parameters. The use of the model is exemplified in the context of participatory modelling where stakeholders have specified how environmental variables affect the stock dynamics of Central Baltic herring (*Clupea harengus membras*).

Résumé : Nous avons développé un modèle générique d'espace d'états structuré selon l'âge pour l'évaluation des stocks qui peut être utilisé comme plateforme pour l'intégration d'information obtenue de parties prenantes. Le modèle suit la taille moyenne en fonction de l'âge et l'utilise pour expliquer les taux de mortalité naturelle et par pêche. La sélectivité de la pêche est divisée en deux composantes, ce qui permet de modéliser la recherche active par la flotte de poissons d'une certaine taille ainsi que la sélectivité de l'engin. Le modèle peut tenir compte d'incertitudes dont les modèles les plus récents d'évaluation intégrée ne tiennent pas compte, à savoir : (*i*) la forme de la fonction stock–recrutement est considérée comme étant incertaine et est traitée grâce à la combinaison bayésienne des estimations; (*ii*) outre les variations de recrutement, les variations de la mortalité naturelle, des paramètres de croissance et de la mortalité par pêche peuvent être traitées comme des paramètres incertains. Un exemple d'application du modèle dans un contexte de modélisation participative où les parties prenantes décrivent l'incidence des variables du milieu sur la dynamique des stocks de harengs (*Clupea harengus membras*) du centre de la mer Baltique est présenté. [Traduit par la Rédaction]

Introduction

Stakeholder knowledge is increasingly identified as an important component in successful fisheries management (Garcia and Charles 2007; Röckmann et al. 2012; Haapasaari et al. 2012), but if stakeholder views of the causal structures differ, how can they all be fairly accommodated in the same model?

While existing stock assessment models are highly sophisticated, they have limited possibilities for the inclusion of alternative hypotheses about model structures, especially when the hypotheses consider inclusion or exclusion of environmental covariates (Kuparinen et al. 2012). The state of the art in stock assessment modelling is to use integrated assessment models (Methot and Wetzel 2012). These are preferably state-space models (Newman et al. 2006), where both the process and observation uncertainty are accounted for and many types of data can be integrated (Kuparinen et al. 2012; Methot and Wetzel 2012; Punt 2003). Stock Synthesis (SS) (Methot and Wetzel 2012), Coleraine (Magnusson and Hilborn 2007), and CASAL (C++ algorithmic stock assessment laboratory; Bull et al. 2002) are perhaps the most advanced and most widely used existing assessment tools representing this category (Kuparinen et al. 2012; Methot and Wetzel 2012).

However, these approaches have restrictions when it comes to the modelling of the process variation. CASAL and SS allow uncertainty about the recruitment variability, but do not allow for uncertainty about any other process variances (Methot and Wetzel 2012; Bull et al. 2002). In SS there can be process variation in somatic growth, natural mortality, and catchability, but the variances of these random effects must be prespecified. In CASAL the population dynamics are deterministic after recruitment. Coleraine allows for random effects in recruitment and catchability, but the variance of these random effects must be prespecified by the user and can thereafter be point-estimated iteratively. CASAL and SS can incorporate explanatory variables for some of the model parameters. In particular, SS has a wide variety of possibilities for the environmental link, but the drawback is that the use of covariates cannot be combined with random effects, even if the random effect variance was fixed (Methot and Wetzel 2012).

Uncertainty about appropriate model structure often dominates the inference about the stock status and dynamics (Kuparinen et al. 2012; Punt and Hilborn 1997). This can be particularly relevant when alternative model structures have been specified by different stakeholders. The modelling tools reviewed above can be used to partly address this problem by repeating the analysis for each combination of plausible structural assumptions and then aver-

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Fig. 1. Map of the Baltic Sea, showing the ICES assessment areas. The example stock inhabits Areas 25–29. The figure was provided courtesy of ICES.
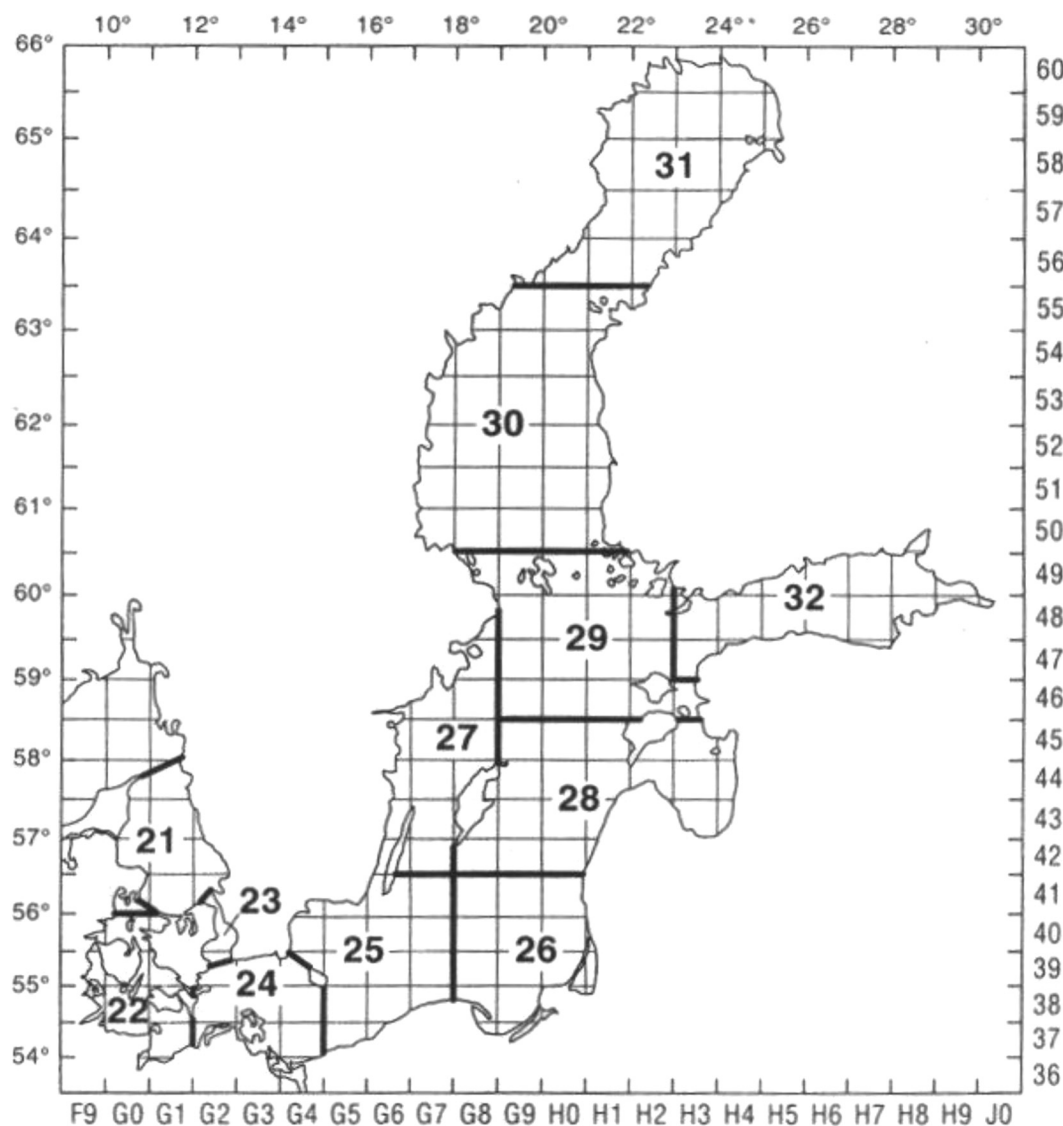
aging the posterior densities obtained from each model run. However, in the same way that not all parameter values are equally credible based on prior information and interpretation of data, not all models are equally credible after assuming the likelihood functions and seeing the data. This should be taken into account when averaging the models.

As suggested by Hammond and O'Brien (2001) and Mäntyniemi et al. (2013), one approach is to treat the alternative causal beliefs as Bayesian models and then use Bayesian model averaging (Hoeting et al. 1999) to account for the uncertainty by updating the relative credibilities of the models based on observed data. However, such a full accounting of model uncertainty is not possible in any of the three modelling frameworks reviewed above.

Bayesian model averaging for different structural assumptions has been used mainly for the stock–recruitment analysis in isolation from the integrated state-space model (Michielsens and McAllister 2004; Pulkkinen and Mäntyniemi 2013; Hillary et al. 2012) and for regression applications (Mäntyniemi et al. 2012). Patterson (1999) included Bayesian model averaging into an integrated assessment model, but after recruitment the model was deterministic. Mäntyniemi et al. 2009 used a fully stochastic population dynamics model where the random effect variances were

treated as uncertain parameters and the form of stock–recruitment function was treated as unknown in the same way as in Patterson 1999.

In this paper we continue the development of integrated assessment models by combining many of the features of widely used assessment models such as CASAL, SS, and Coleraine with the possibility to account for model uncertainty, unknown process variances, and environmental covariates at the same time.

As an example, we apply the model to the Baltic Sea main basin herring (*Clupea harengus membras*) stock (herring in ICES subdivisions SD 25–29 and 32, excluding the Gulf of Riga; Fig. 1). Its assessment for fisheries management purposes within ICES currently applies Extended Survivors Analysis (ICES 2009), supported with acoustic surveys. It has been estimated that considerable changes have taken place in abundance, mass-at-age, and fishing mortality of herring in the Baltic Sea main basin (ICES 2009). Environmental covariates that might be driving these changes were the focus of Mäntyniemi et al. (2013) and Haapasaari et al. (2013). They developed a structured interview that was used to elicit the knowledge of stakeholders and experts and encode them into probability statements about external factors that affect the dynamics of a fish stock. However, it turned out that

Fig. 2. Schematic presentation of the model structure.
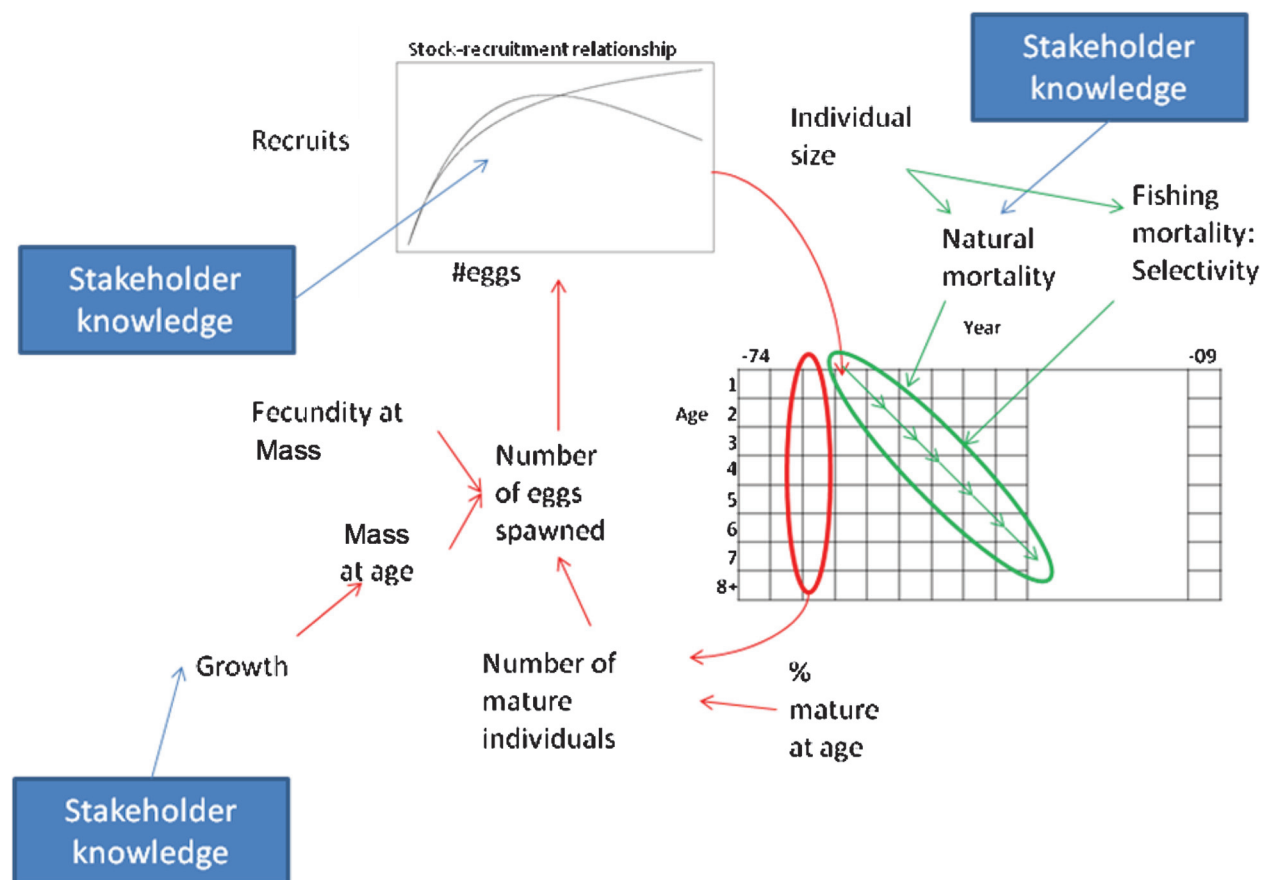
eliciting the structure of the entire assessment model from a set of stakeholder representatives would be a daunting task, and a mixed approach where a ready-made model framework is used as a basis was thought to be more feasible (Mäntyniemi et al. 2013). In this approach, the basic components of population dynamics was specified by a small group of researchers, and the model was then presented to a group of stakeholders whose next task was to elucidate their beliefs about the external factors driving the dynamics. The group of stakeholders also included fishery scientists, whose views were treated equally with other persons. In this paper we present the population dynamics model that was designed to be able to accommodate the different views of the stakeholders. The example analysis includes the prior knowledge elicited from one of the fishery scientists who participated in the study. The results of model averaging over all the 432 possible combinations of alternative model structures are presented in Mäntyniemi et al. (2013).

Materials and methods

Data
Our primary source of data are the data set used by the ICES Baltic Fisheries Assessment Working Group (WGBFAS). The data set consists of age-specific commercial catches from years 1974–2007, mean mass-at-age (1974–2007), and acoustic survey estimates (1982–2007).

Model structure
The general characteristics, their justifications, and information sources are presented below; the mathematical specification of the model and its parameters can be found in Appendix A.

The model consists of age-structured population model and a stock–recruitment relationship model (Fig. 2). The population

model features three key parameters where external factors can be used to drive the dynamics: somatic growth rate, natural mortality rate (which depends also on individual size), recruitment, and annually varying size-dependent fishing mortality. The stock size and structure (number of individuals at each age and average mass-at-age) are estimated based on the catch-at-age and mass-at-age data and yearly growth and mortality rates. The strength of year class 1 is estimated based on the stock–recruitment model, and in consecutive years, the catch-at-age information serves to enhance the estimate of the year-class strength.

Growth and mortality
Individual growth follows the von Bertalanffy curve and is modeled as mean length-at-age for each year separately. Unlike SS, CASAL, and Coleraine, the growth has two random components: a year effect as annually varying growth rate and an age-specific annual random deviation. The variances of both random effects are treated as uncertain, estimable parameters with priors. The expected annual growth rate is specified as a log-linear function of environmental covariates, where the priors for the regression coefficients have been elicited with the method described in Mäntyniemi et al. (2013). In this case the zooplankton abundance, sea surface temperature, and sprat (*Sprattus sprattus*) abundance were identified as explanatory factors.

Mean mass-at-age is computed from the mean length-at-age based on observations from an adjacent sea area, the Bothnian Sea (H. Peltonen, unpublished data). For simplicity, no uncertainty is assumed in this relationship, as it is very minor compared with other uncertainties.

The natural mortality is age-specific and is assumed to vary randomly from year to year, with annual mean depending on mean mass-at-age and environmental covariates specified by the

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stakeholder. The expected natural mortality is also assumed to decrease as individual mass increases (Beyer 1989), as suggested by Gislason et al. (2010). Our stakeholder specified a prior that states that in addition to body mass, cod biomass would also affect the natural mortality.

Fishing mortality varies across years and ages according to a two-way hierarchical model. There is a year effect that can be seen to reflect annual changes in fishing pressure, and the annual age effect describes the stochasticity of the fishing process arising from different factors, such as schooling (Ruttan 2003; Lindén and Mäntyniemi 2011). Variances of the random effects between and within years are treated as uncertain parameters. The fishing mortality of each age group each year is assumed to depend on two things: the availability of fish in the main fishing areas and the selectivity of the trawls. The first component accounts for the fact that the herring spawn at the shore, and the juvenile individuals need to migrate to the open water to join the school. Therefore, the youngest and smallest fish are not where the fishery takes place. This was represented using a sigmoid curve for the availability of fish to the fishery as a function of the body length. The mechanical trawl selection accounts for the fact that the smallest individuals may slip through the trawl mesh. The priors of the trawl selection curve were based on Suuronen and Millar (1992) and Rahikainen et al. (2004). Small uncertainty was allowed for the selection curve parameters reported by these papers.

The herring are fragile, and even though the smaller individuals escape through the trawl codend, 77%–100% of them die during the subsequent 14-day period (Kuikka et al. 1996; Suuronen et al. 1996a, 1996b). Traditional virtual population analysis (VPA) methodology doesn't take into account the fact that these individuals are removed from the population even though they do not show in the catch statistics, which may result in biases in stock–recruitment curve estimation, since it has a direct effect on recruitment estimates (Rahikainen et al. 2004). In the present model, we assume that 100% the escaped individuals die.

Reproduction

The fecundity of fish is known to vary, for example, because of demography of the stock and size and quality of the parents (Marshall 2003; Lambert 2008; Morgan 2008). Major changes in the average body size have been observed in the currently studied stock (ICES 2009). The spawning stock biomass might not give an unbiased picture of the real spawning potential. Therefore, the stock–recruitment function is defined here on the basis of spawned eggs rather than spawning stock biomass. This allows the explicit consideration of changes in the population structure that affect the average fecundity per mass. The fecundity per mass of the female herring is assumed to increase as mass increases (e.g. Wootton 1990). The functional form, as well as priors for its parameters, are based on empirical studies conducted in the Inkoo area in the northern part of the Main Basin by Parmanne and Kuittinen (1991).

Recruitment is assumed to follow either Beverton–Holt or Ricker stock–recruitment curves; the relative probabilities of these models are estimated within the model run as in Mäntyniemi et al. (2009). The recruitment curves are parameterized so that the parameters represent the slope at the origin and the (asymptotic) maximum of the curve. Both of these parameters have a biologically meaningful interpretation, making it possible (if not easy) to assign priors based on biological understanding from published papers and stock assessments made in other areas, if they include the same estimation of model probabilities (e.g., Pulkkinen and Mäntyniemi 2013). In this case both functional forms were assumed to be equally likely a priori.

The slope at the origin corresponds directly to the survival rate of eggs in very low egg densities, as in Methot and Wetzel (2012) and Pulkkinen and Mäntyniemi (2013). The prior for survival was based on the following consideration. The instantaneous daily mortality rate of marine pelagic and demersal eggs are of the order 1.0 to 0.04, corresponding to respective daily survival rates of 37% to 96% (McGurk 1986; Wootton 1990), and that of larvae are 0.78 to 0.06, corresponding to respective daily survival rates of 46% and 94%. The daily instantaneous mortality rates of juveniles and adults are strongly dependent on the fish size and vary between 4.6×10^{-2} and 1.5×10^{-4}, corresponding to daily survival rates of 95.5% and 99.99%, respectively (McGurk 1986). The prior was chosen to be informative in the sense that it strongly proposes values smaller than 5×10^{-4}, but is relatively uninformative on this range. The annual deviations of the recruitment compared with the expected value given by the uncertain egg–recruitment function were modelled using a log-linear regression with environmental covariates and annual random effects. Priors for the regression coefficients were elicited from the stakeholder, and a vague prior was assigned to the variance of the random effects. According to the stakeholder, sea surface temperature, cod stock biomass, sprat stock biomass, and zooplankton abundance would explain the recruitment, in addition to number of eggs spawned.

Posterior computation

The model was fitted to ICES stock assessment data using Markov chain Monte Carlo (MCMC; e.g., Gilks et al. 1996) estimation of the joint posterior distribution of model parameters. The simulation was implemented using Just Another Gibbs Sampler (JAGS; Plummer 2012), which is similar to the commonly used WinBUGS software. JAGS was preferred over BUGS because we have found it faster and numerically more stable. Also, the model averaging over competing model structures was implemented within a single MCMC run by adopting the approach introduced by Carlin and Chib (1995). Thus, the complications of Reversible Jump MCMC (Green 1995) were avoided, and the analysis could be completed using generic MCMC software. The JAGS and R code needed to run the analysis presented here is available as an electronic supplement[1]. As with all integrated assessment frameworks, adapting the model to a new case requires case-specific knowledge about appropriate biological model structures, priors for population dynamic parameters, and knowledge about appropriate statistical sampling models for observed data. Some knowledge about BUGS–JAGS model specification syntax is also needed. The JAGS software takes care of the MCMC sampling algorithms; they do not have to be designed and tuned by the user.

The MCMC run consisted of four independent MCMC chains run on separate processor cores on 2.8 GHz Intel Xeon processor. Generation of 5 000 000 samples took about 13 h. All the chains were thinned by saving only every 500th sample. The nonconvergence of the chains was then examined based on the remaining 10 000 samples. Based on visual inspection of the chains, running means, and Gelman–Rubin diagnostic plots (Brooks and Gelman 1998), the first 6000 samples were treated as the burn-in period. The remaining 4000 samples from each chain were merged to form a sample of 16 000 that was used for posterior inference.

Results

The relative availability of fish of different sizes to the fishery was not well known a priori. However, this function becomes quite precisely estimated based on data and prior knowledge about other parameters (Fig. 3). This information can be seen to arise as a combination of knowledge about other size-based functions and observed age and size distributions in the catch. The

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Fig. 3. Relative availability of herring to the fishery as a function of length. The availability is scaled so that at 28 cm the availability = 1. Lines have been randomly drawn from the posterior distribution to depict the associated uncertainty.
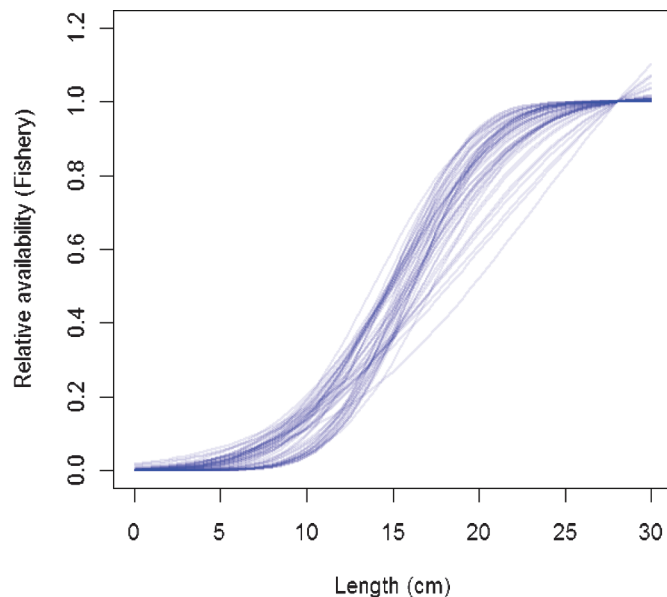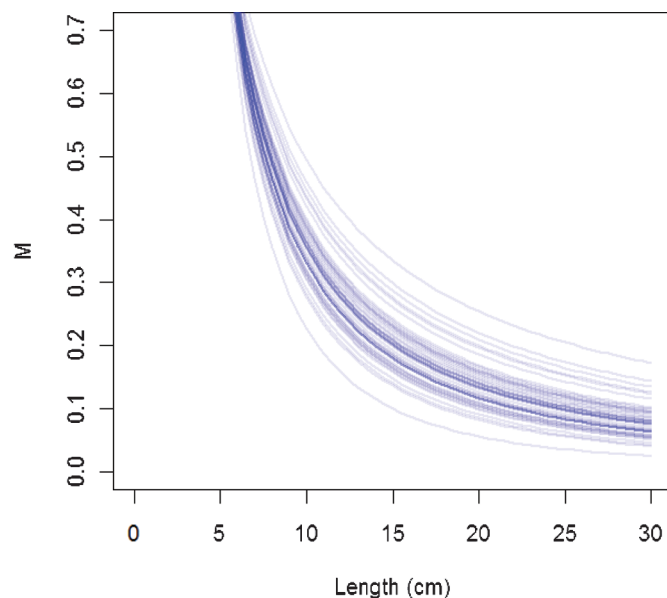

Fig. 4. Estimated natural mortality (*M*) presented as a function of length. The model specifies the natural mortality as a function of mass, environmental covariates, and random effects. This plot shows the size-based component after converting mass to length. Lines have been randomly drawn from the posterior distribution to depict the associated uncertainty.

Fig. 5. Instantaneous natural mortality at ages 1 and 5. Black lines represent the values assumed in the ICES stock assessment. Transparent grey lines are random draws from the joint posterior distribution of the model parameters. As a result, the areas with higher probability density are shaded with darker color.

Fig. 6. Total biomass of the herring stock (upper panel) and average fishing mortality over ages 3–7 (lower panel). Black solid lines are values from the ICES stock assessment. Transparent grey lines are random draws from the joint posterior distribution of the model parameters. As a result, the areas with higher probability density are shaded with darker color.
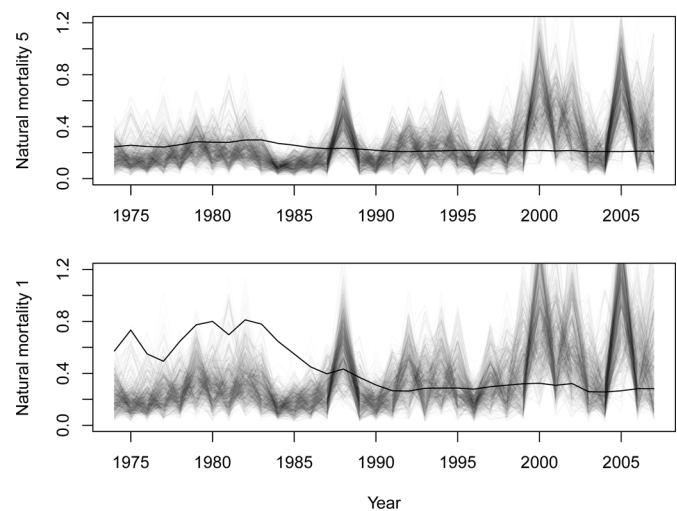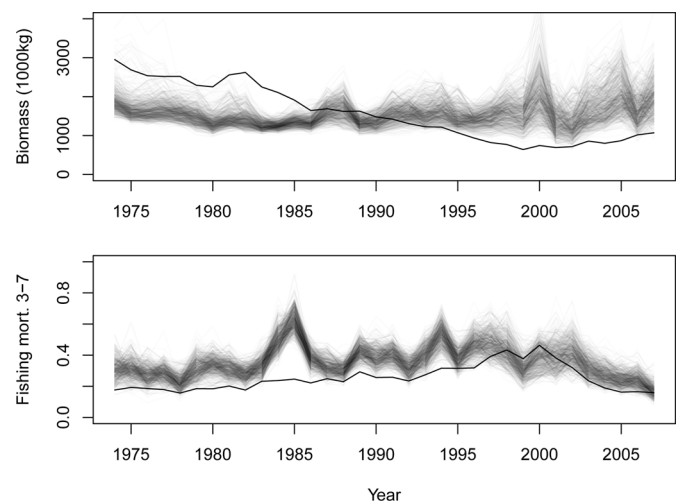

mechanical selectivity of the gear was well known, which makes it possible to infer the size–age distribution of fish that encountered the fishery. Another important piece of information is the size dependency of natural mortality rate (Fig. 4), which gives the age–size distribution expected in the population.

The estimates of natural mortality are clearly different compared with ICES stock assessment (Fig. 5). The ICES values are based on the assumption of background mortality of 0.2 and additional mortality caused by cod predation based on multispecies VPA (ICES 2009).

However, the biggest difference in policy implication comes from the fact that there is no decreasing trend in total biomass, as in the case of ICES assessment (Fig. 6). Overall the fishing mortality is estimated to have been higher than estimated by ICES, with a notable peak in mid-1980s. In contrast with the ICES assessment, the total biomass is estimated to have been quite stable. The decrease in mean mass-at-age (ICES 2009) combined with the nonlinear relationship between mass and fecundity leads to a decreasing trend in egg production (Fig. 7). The annual variation in recruitment resembles the ICES estimates, but the trend and magnitude of the variation are highly different. The annual variation in recruitment is quite well explained by the environmental covariates, and the fit is clearly better under the Ricker than the Beverton–Holt function (Fig. 7). This difference is also reflected in the relative credibilities of these functions; the posterior probability of the Ricker is 0.93 and is 0.07 for the Beverton–Holt.

Fig. 7. Number of eggs spawned (upper panel) and number of resulting recruits (lower panel). Solid black line shows the recruitment estimated by ICES. ICES estimates for the number of eggs do not exist. Transparent grey lines are random draws from the joint posterior distribution of the model parameters. As a result, the areas with higher probability density are shaded with darker color. Red line shows the posterior mean of expected recruitment based on the Ricker function and environmental covariates. Blue line shows the posterior mean of expected recruitment based on the Beverton–Holt function. The annual recruitment shown with shaded grey is a model-averaged estimate, which also includes the random effects in the recruitment process.

Fig. 8. Estimated stock–recruitment relationship for Central Baltic herring. Black dots represent posterior medians of egg–recruitment pairs. Transparent red circles are random draws from the posterior distribution of two pairs (2002–2003 and 1974–1975) depicting the uncertainty associated to both egg and recruitment estimates. Each pair has similar uncertainty, but these are not shown for the sake of clarity. Grey transparent lines are random draws from the posterior distributions of stock–recruitment parameters, drawn according to posterior probabilities of the alternative model structures.
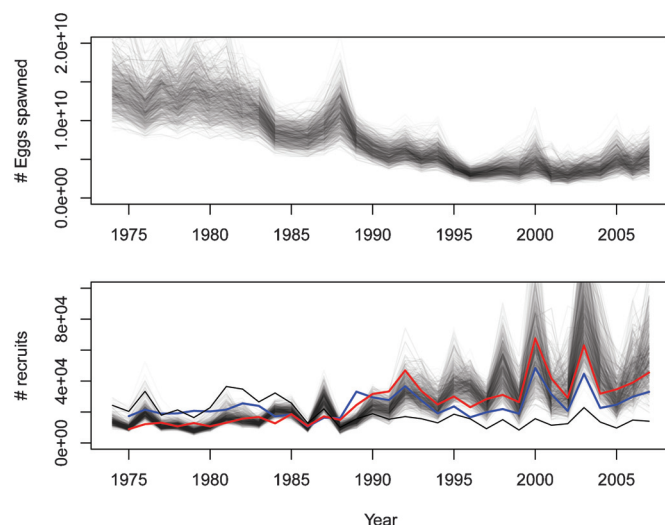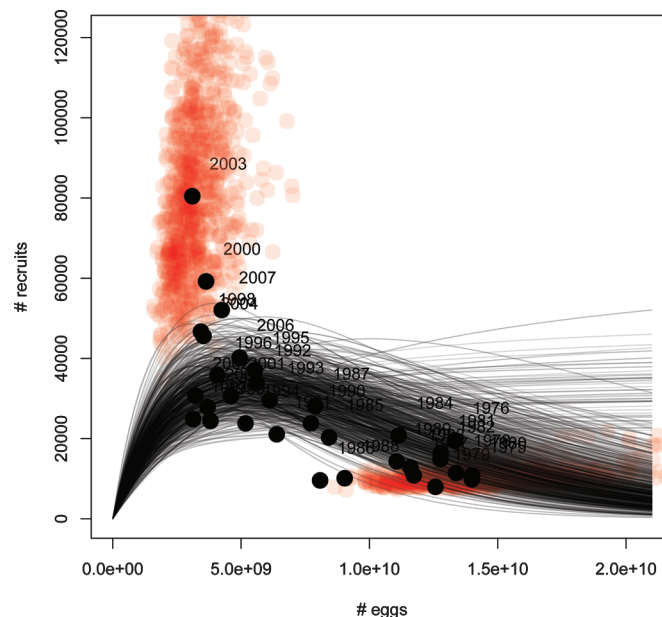

Figure 8 illustrates the prevailing uncertainty about the egg–recruitment pairs and fitted stock–recruitment function. Uncertainty about the expected recruitment is highest for high egg abundances, from which less information exists. Figure 9 shows the priors and posteriors of the six different process error variance parameters that are used to describe the stochastic processes in the population dynamics. Posterior correlation of these parameters were practically zero (not shown).

Discussion

This paper presents a modern approach to stock assessment, made possible by the increased computing power and recent development in statistical computing. This approach integrates all available knowledge into the stock assessment scheme, including the best available estimates of the uncertainty related to this information. Unlike most integrated assessment models, our approach is capable of estimating the posterior distribution of multiple process error variance parameters while accounting for structural uncertainty and environmental covariates at the same time.

Our results differ markedly from those of ICES, which are currently used in the policy of Baltic Sea herring management. There is an obvious need to start analysing all possible data sets, including commercial catch-per-unit-effort (CPUE) data sets that do exist in EU member countries to be able to look at the catcabilities of commercial and survey vessels separately. This may help to improve estimates of fishing mortality, and at least we would understand better the dynamics of commercial fleet and their impact on selectivities. Moreover, the model priors for the stock–recruitment function should preferably come from other assessments of herring and similar kinds of stocks, as the stock–recruitment function is crucial for future risk simulations and when estimating the recovery potential of the stock in case of

assessment and (or) management error, i.e., if we fail to estimate the trend correctly and the stock must be recovered.

The purpose of a Bayesian stock assessment model is to quantify the knowledge about the state and population dynamic parameters of a fish stock realistically or honestly (Mäntyniemi et al. 2009). To achieve this, the model is constructed based on as plausible biological assumptions as possible, the existing knowledge about the model structure and parameters is gathered from as many sources as possible, and all the available data are utilized as extensively as possible. In other words, the model structure and the number of unknown parameters depend primarily on biological knowledge about the species and on the knowledge about the survey design and behavior of the fishing fleets (Methot and Wetzel 2012). This type of "modelling" approach can be contrasted with the more classical "data analytic" approach where the complexity of the model is mostly driven by the amount of data available to estimate the model parameters (Kuparinen et al. 2012).

Many of the papers that present Bayesian stock assessment models argue that one of the advantages of the approach is the possibility to explicitly utilize the existing knowledge in the form of prior distributions. However, quite often the same papers only deal with the question of how to not include such information, i.e., how to define a vague or minimally informative prior distribution. This is understandable in the sense that each real life problem is different, and consequently the prior distribution must always be case-specific; it is difficult to give universal recommendations about any other type of prior distribution than a vague prior. On the other hand, such a practice may prevent accumulation of experience and discussion about the admittedly difficult process of defining the informative prior. In this paper we tried to initiate a different practice by devoting a considerable amount of space for describing how we derived the prior distributions used in the case study of Baltic herring.

Fig. 9. Prior (thin line) and posterior (bold line) distributions of process error variances expressed as coefficients of variation (CV). CVR = CV of recruitment random effects; CVM = CV of natural mortality random effects; CVyF = CV of fishing mortality year effects; CVaF = CV of fishing mortality age effects; CVL = CV of random effects for length increments; CVk = CV of annual growth rate random effects.
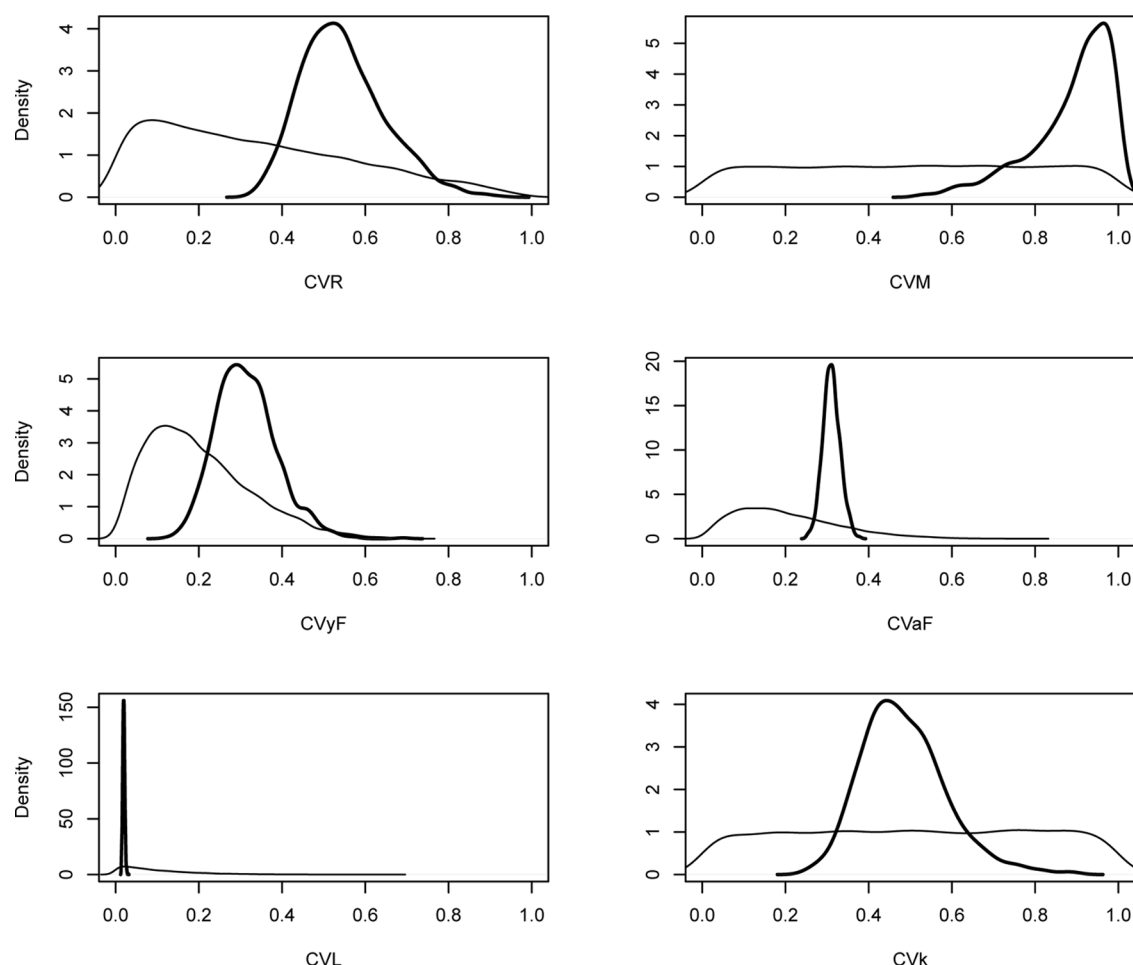
The current paper presents the foundations of a customizable, extendable stock assessment model. It can be applied to many fish stocks with age-structure information. The model components such as fecundity, maturity, and growth functions can be changed to match the given situation without having to change the core dynamics. Also, the data used with the model can take many forms. For example, the model can be fitted to catch data only or survey data only. Age and size distributions can also be included or excluded at will. With the state-space model structure, any new kind of data can be included by formulating a suitable observation model, which makes the model very general. In this regard it is quite similar to other integrated assessment models, such as SS (Methot and Wetzel 2012). An interesting future line of research would be the comparison of inferences drawn from the same data set using different integrated assessment models while using as similar assumptions as possible.

The model presented here has a couple of obvious issues that can be improved, which are mostly related to how growth is modelled. First, the fact that the model tracks the mean length-at-age instead of full length distribution means that fish with different growth rates are not properly selected from the population by fishery and natural mortality. A related issue is that when the selectivity of growth rates is not accounted for, the slow change in the distribution of growth parameters in the population that would result from size-selective fishing cannot be accounted for at all. A potential way to improve this part of the model would be to inherit growth parameters to each year class based on the distri-

bution of growth parameters in the spawning cohorts in the previous years. Another approach could be to divide the population into groups with different growth parameters as in SS (Methot and Wetzel 2012) and CASAL (Bull et al. 2002).

The effective sample size of 1000 for the age composition data with multinomial likelihood was assumed in our example analysis. This area deserves more attention in the future so that uncertainty also about this parameter could be admitted and then accounted for. Methods developed by Hulson et al. (2011, 2012) could be included in future versions of the model.

The time- and age-varying random effects were modelled as white noise on a log scale. This means that unrealistically sudden changes in some of the estimates may occur. More gradual changes could be accommodated by turning the white noise processes into red noise (Ruokolainen et al. 2009) by introducing an autocorrelation parameter for which a prior could be assigned to. After this, a logical step might be to use a Gaussian process layer, which could capture systematic deviations from the assumed functional forms (Munch et al. 2005). Also, expansion to multistock analysis would be potentially very useful (Punt et al. 2011) and can be created in a JAGS model simply by creating a loop over the entire model structure and adding an index for different stocks. This would also be a convenient way to extract information from tag–recapture data by modelling the population of tagged individuals in parallel with the population of interest and couple the models by assuming the same or similar parameters for the two stocks. Some of the parameters could also be different.

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For maximum use of all available information, the correlations between biological parameters could be learned from online databases (Pulkkinen and Mäntyniemi 2013; Froese et al. 2013) and then utilized within the multistock analysis where all the stocks are fitted to their data sets while keeping a hierarchical structure with hyperparameters.

Acknowledgements

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Appendix A. State-space model structure

Population dynamics and biological functions

This appendix contains the mathematical specification of the assessment model. The choice of parameterization is heavily impacted on the practical aspect of being able to fit the model using MCMC simulation. This requires suitable choices of distributions that describe population transition from one time step to the next. The performance of the MCMC is also greatly enhanced by scaling the abundances so that they are relative to the abundance in the first year.

The total population size N_y evolves in time as

$$N_{y+1} = N_y\delta_y + R_{y+1}$$

where δ_y is the mean survival of individuals over year y, and R_{y+1} is the number of new recruits entering the population in year $y + 1$. To improve MCMC we set $N_1 = 1$ and define N^* as the true population size at time $y = 1$ for which a prior distribution must be assigned. Thus, the absolute population size at any time can be obtained as N_yN^*.

The annual mean survival is obtained as

$$\delta_y = \sum_{a=1}^{A} p_{y,a}\exp(-Z_{y,a})$$

where $p_{y,a}$ is the proportion of individuals of age a, and $Z_{y,a}$ is the total annual instantaneous mortality rate, assumed to be constant throughout the year. The change in the age distribution during a time step is then given by

$$p_{y+1,a+1} = \frac{p_{y,a}\exp(-Z_{y,a})}{\delta_y}(1 - p_{y+1,1}), \quad a = 1,\ldots,A-2$$

$$p_{y+1,A} = \left[\frac{p_{y,A-1}\exp(-Z_{y,A-1})}{\delta_y} + \frac{p_{y,A}\exp(-Z_{y,A})}{\delta_y}\right](1 - p_{y+1,1})$$

$$p_{y+1,1} = \frac{R_{y+1}}{N_{y+1}}$$

This is obtained simply by dividing the age-specific abundances by the total abundance. Working on the relative scale instead of absolute numbers helps the convergence of the MCMC simulation.

The total mortality is composed of fishing mortality and natural mortality: $Z_{y,a} = F_{y,a} + M_{y,a}$. The natural mortality is assumed to depend on mean mass-at-age ($w_{y,a}$) as follows:

$$M_{y,a} = w_{y,a}^{-G}\exp(\epsilon_{M,y})$$

$$\epsilon_{M,y} \sim N\left[\log(\mu_{M,y}) - 0.5\sigma_M^2, \sigma_M^2\right]$$

$$\sigma_M^2 = \log(C_M^2 + 1)$$

where constant G and coefficient of variation C_M^2 are given prior distributions. In the absence of environmental covariates, the expected value of random effect can be assumed constant: $\mu_{M,y} = 1$. The environmental covariates can be included by formulating a suitable regression model for $\mu_{M,y}$.

The fishing mortality is assumed to depend on three components: variation in overall fishing pressure changing from year to year, size selectivity of the fishing fleet (availability), and random process deviations from the expected fishing mortality. Thus,

$$\log(F_{y,a}) \sim N\left[\log(F^{\text{median}}) + \log(v_{y,a}) + \epsilon_{F,y}, \log(C_{F,1}^2 + 1)\right]$$

$$\epsilon_{F,y} \sim N\left[0, \log(C_{F,2}^2 + 1)\right]$$

where F^{median} is the median fishing mortality across years and is assigned a prior distribution. Random effects $\epsilon_{F,y}$ describe variation in overall fishing mortality around the median with coefficient of variation $C_{F,2}$. Age-specific deviation from expected fishing mortality is defined by coefficient of variation $C_{F,1}$. Both CVs require a prior distribution. Selectivities $v_{y,a}$ describe the availability of different age groups to the fishery. These are modelled using a probit-regression model, which is scaled to 1 for 28 cm long fish:

$$v_{y,a} = \frac{\Phi\left[(l_{y,a} - V_{50})/V_{SD}\right]}{\Phi\left[(28 - V_{50})/V_{SD}\right]}$$

where $\Phi()$ is the cumulative distribution of a normal distribution, $l_{y,a}$ is the mean length-at-age, V_{50} is the length with steepest change in selectivity, V_{SD} describes the softness of the selection curve, and $V_{50} \pm 2V_{SD}$ can be interpreted as the length interval where selectivity increases from very small to full.

The probability γ_y that a fish gets caught by fishery is modelled using the conventional Baranov catch equation:

$$\gamma_y = \sum_{a=1}^{A} s_{y,a}\frac{F_{y,a}}{Z_{y,a}}[1 - \exp(-Z_{y,a})]p_{y,a}$$

where $s_{y,a}$ is the mechanical selectivity of the fishing gear. Consequently, the expected age distribution in the catch can be obtained as

$$\pi_{y,a} = s_{y,a}\frac{F_{y,a}}{Z_{y,a}}[1 - \exp(-Z_{y,a})]p_{y,a}/\gamma_y$$

The mechanical selectivity of the whole fishery is calculated as weighted average of the selectivity curves of the different gears used in the fishery:

$$(1) \qquad S_{y,a} = \sum_{i=1}^{n} g_{y,a,i}q_{y,i}$$

where $g_{y,a,i}$ is the mechanical selectivity of gear i, and $q_{y,i}$ is the proportion of that gear used in year y. This follows from the law of total probability where conditional probability of getting selected when encountering gear i and proportions of different gears give the probability of encounter. Prior distribution is required for the vector of proportions. In the case of Baltic herring, the selectivity is modelled using a logistic function

$$\log\left[g_{y,a,i}/(1 - g_{y,a,i})\right] = \alpha_i + \beta_il_{y,a}$$

where α_i and β_i are known from selectivity experiments.

The mean length-at-age is assumed to change according to the von Berttalanfy growth curve with normally distributed random deviations:

$$\log(l_{y+1,a+1}) \sim N\left(\log\{L_{\text{inf}} - l_{y,a}[1 - \exp(-k_y)] + l_{y,a}\}, \sigma_L^2\right)$$

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where L_{inf} is the asymptotic size assumed to be constant over years, and k_y is the annual growth rate assumed to vary between years according a hierarchical model

$$\log k_y \sim N\big(\mu_k, \sigma_k^2\big)$$

where μ_k is the mean of the log(growth rate) across years, and variance σ_k^2 represents variation of growth rate between years. Both parameters require a prior distribution. Environmental effects can be modelled by formulating a regression model for μ_k.

The mean mass-at-age is assumed to depend on mean length-at-age according to the widely used log-linear relationship

$$\log(w_{y,a}) \sim N\big[a_w + b_w \log(l_{y,a}), \sigma_w^2\big]$$

where regression parameters and the residual variance must be assigned a prior distribution.

The total number of eggs spawned in each year is calculated as

$$E_y = \frac{N_y r}{\psi_y} \sum_{a=1}^{A} w_{y,a} m_{y,a} f_{y,a} \exp(-Z_{y,a}h) p_{y,a}$$

$$\psi_y = \sum_{a=1}^{A} \exp(-Z_{y,a}h) p_{y,a}$$

where r is the proportion of females in the population, $m_{y,a}$ is the proportion of mature females at age, $f_{y,a}$ is the number of eggs per female unit of mass, h is the relative time from the beginning of the year to spawning, and ψ_y is the proportion of fish that survive to the spawning time. All of these parameters require a prior distribution. In the Baltic herring case, the spawning time, ratio of females, and the maturity ogive were assumed to be known without error. Fecundity was modelled using a log-linear curve with priors for the parameters formulated based on existing literature.

The number of recruits is modelled as a log-normal process

$$\log(R_{y+1}) \sim N\big[\log\big(E_y \mu_{R,y}^{\mathrm{model}}\big) - 0.5\sigma_R^2, \sigma_R^2\big]$$

where the expected value is interpreted as density-dependent survival of eggs, having two possible functional forms:

Model 1:
$$\mu_{R,y}^{\mathrm{model}=1} = \frac{K}{K/\alpha + E_y} \exp(\epsilon_y)$$

Model 2:
$$\mu_{R,y}^{\mathrm{model}=2} = \alpha \exp\left[\frac{-\alpha E_y}{K \exp(1)} + \epsilon_y\right]$$

where model = 1 has the form of Beverton–Holt function, and model = 2 is the Ricker function. Both functions are parameterized in terms of the survival of eggs (α) in very low egg density and maximum number of recruits (K). Both of these parameters and the residual variance σ_R^2 require prior distributions. Parameter ϵ_y can be used to incorporate effects of environmental covariates by formulating a regression model for it. Uncertainty about the shape of the survival function must be expressed by prior probabilities $P(\mathrm{model} = 1)$ and $P(\mathrm{model} = 2) = 1 - P(\mathrm{model} = 1)$.

Observation models

This section describes the statistical models that link the underlying stock dynamics to the observable data in the Baltic sea herring case.

Mass-at-age
Mass-at-age is assumed to be observed without an error.

Total catch in tonnes
The mass of total catch is given by $C_y = N_y N^* \gamma_y \sum_{a=1}^{A} w_{y,a} \pi_{y,a}$, and the observed catch is assumed to have a random annual error with CV = 0.05:

$$\log\big(C_y^{\mathrm{obs}}\big) \sim N\big[\log(C_y), \log(0.05^2 + 1)\big]$$

Age distribution in catch
The observed age distribution in catch $(x_{y,1}, \ldots, x_{y,A})$ is assumed to have on effective sample size of 1000, thereby the age frequencies samples from the catch are first scaled to sum up to 1000 and then assumed to follow a multinomial distribution given the expected age distribution from the population dynamics model

$$x_{y,1}, \ldots, x_{y,A} \sim \mathrm{multinomial}(1000, \pi_{y,1}, \ldots, x_{y,A})$$

Age distribution in the scientific survey
The expected age distribution in the survey is given by

$$\omega_{y,a} = \frac{z_{y,a} p_{y,a} \exp(-Z_{y,a}c)}{\sum_{a=1}^{A} z_{y,a} p_{y,a} \exp(-Z_{y,a}c)}$$

where $z_{y,a}$ is the probability that a fish of age a gets observed by the survey, and c is the time relative time of the year when survey is conducted. The survey selectivity is modelled using a probit-regression model in the same way as the availability selectivity of the fishery. The observed age distribution in the survey is assumed to follow a multinomial distribution with effective sample size of 1000:

$$d_{y,1}, \ldots, d_{y,A} \sim \mathrm{multinomial}(1000, \omega_{y,1}, \ldots, \omega_{y,A})$$

The biomass B_y observable by the survey is given by

$$B_y = N_y N^* \sum_{a=1}^{A} w_{y,a} \omega_{y,a}$$

and the observed survey result is then assumed to have uncertain bias (b_{survey}) and variability (C_{survey}^2):

$$\log\big(B_y^{\mathrm{obs}}\big) \sim N\big[b_{\mathrm{survey}} + \log(B_y) \\ - 0.5\log\big(C_{\mathrm{survey}}^2 + 1\big), \log\big(C_{\mathrm{survey}}^2 + 1\big)\big]$$