

Modelling the effect of ecosystem change on spawning per recruit of Baltic herring

Mika Rahikainen, Sakari Kuikka, and Raimo Parmanne

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A plea for linking assessment and management to the broader ecosystem state has been made several times in the fisheries literature. The need for ecosystem considerations is obvious for Baltic herring stock which has experienced large fluctuations in growth and natural mortality rate. Biological reference points, based on stock-recruitment data, have gained importance under precautionary approach and the need for more restrictive management. An alternative method for establishing thresholds for recruitment overfishing is spawning per recruit analysis. Within this context, understanding the effects of highly variable natural mortality and growth rate on fishing mortality reference point is of interest. We used Monte Carlo simulations to investigate variation in spawning per recruit caused by varying stock attributes. Causal biological response to changing environmental conditions was created by adjusting the correlation between growth, maturity, and natural mortality. The correlation of the input variables was controlled under three models, assuming future conditions were (1) as experienced recently (empirical model), (2) random, and (3) depending upon causal linkages in the biological key processes (ecological model). The overall uncertainty was large in all models. Biological reference point ($F_{30\%SPR}$) was uncertain due to problem of defining maximum spawning per recruit and due to variation in input variables in SPR analysis. The concept of $F_{x\%SPR}$ was judged to be ambiguous. The use of causal ecological knowledge reduced uncertainty of the reference point only to a limited extent. However, relying only to the observed data appeared to be the riskiest approach.

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Introduction

The Baltic herring (*Clupea harengus*) stock has experienced large fluctuations in growth and natural mortality during the last two decades (Parmanne, 1992; Sjöstrand, 1992; Anon., 1994; Parmanne *et al.*, 1997). Since 1982–1983, the observed mean weight-at-age has decreased 50% from the maximum values in several age-groups (Stephenson *et al.*, 2001; Cardinale and Arrhenius, 2000). At the same time, relative variation in natural mortality rate among age groups 1 to 3, as estimated from multispecies virtual population analysis (MSVPA),

has been as large as variation in growth rate (ICES, 1999a). Together these changes have affected production per recruit (Kuikka *et al.*, 1996) and are, thus, the major biological factors contributing to risk of stock collapse.

Multispecies interactions may have a strong influence on dynamics of the herring stock in the Baltic periodically, depending on abundance of cod as the main predator in the ecosystem (Rudstam *et al.*, 1994; ICES, 1997a; ICES, 1999b) and sprat as food competitor (Arrhenius, 1995). In addition, bottom-up processes mediated via changes in mesozooplankton species composition may have influenced herring growth (Flinkman

et al., 1998; Vuorinen *et al.*, 1998). All of these processes are affected by the same environmental factor, the Baltic salinity level, which is linked to Baltic inflow and precipitation (Hänninen, 1999). The key question is how predictable these links are in the future. Utilizing increasing biological knowledge would be highly useful in stock assessments (Ulltang, 1996) and in management (Stephenson and Lane, 1995). For long-term stock simulations aiming at studying the effects of different exploitation strategies, assumptions on possible causes of change in maturation schedule, and links between maturity, growth, and mortality are critical (Ulltang, 1996).

For many fish stocks, derived stock-recruitment scatterplots are uninformative and in these cases alternative criteria or information sources must be considered in determining levels of sustainable harvesting. Spawning per recruit (SPR) analysis has received some attention in establishing thresholds for recruitment overfishing (Shepherd, 1982; Sissenwine and Shepherd, 1987; Goodyear, 1993; Mace and Sissenwine, 1993; Myers *et al.*, 1994; Caddy and Mahon, 1995; Cook, 1998). In this analysis, growth, maturity and natural mortality are the essential input variables in conjunction with stock-recruitment data. Reference points are a key concept in implementing a precautionary approach (ICES, 1997b) which has gained acceptance as a basis for fisheries management in the worldwide pursuit of sustainable use of renewable resources (FAO, 1995; Richards and Maguire, 1998). As the fundamental management target is avoiding recruitment overfishing, spawning per recruit analysis gives framework to generate biologically valid reference points.

SPR analysis has been applied to large sets of worldwide stock-recruitment data (Myers *et al.*, 1995) and, moreover, to explore how taxonomic affiliation affects the resilience of a stock (Mace and Sissenwine, 1993). Mace and Sissenwine (1993) used a definition replacement %SPR (F_{rep} ; SPR that is $x\%$ of that with no fishing) for a threshold that is necessary for replacement. Furthermore, they suggested that in the absence of standard stock assessment information (spawning stock size, recruitment, and their relationship) taxonomic affiliation and life history parameters can be used to select preliminary %SPR estimates. This is an advantage for stocks such as Baltic herring which has a history of highly uncertain stock assessments (ICES, 1999b). Due to the uncertainty in assessment output, a stock-recruitment function and maximum recruitment-per-unit-biomass are difficult to determine. As any reference point based on uncertain assessment output is risky, an approach grounded on more general knowledge is preferred in deriving biological reference points (BRP) for this stock.

The conventional input data set for SPR analysis includes stock-recruitment scatterplot derived during

several years of observations combined with a SPR curve. This single SPR curve is calculated from data pooled over all or some recent years using the average weight, maturity, and natural mortality-at-age. The SPR curve, thus, represents the static element and the S-R scatterplot the dynamic element of the analysis in a sense that additional S-R observations may provide new insight about stock dynamics and alter our perception of appropriate reference point definition.

Commonly, stock assessment and prediction use empirically observed parameters and the variation within, but neglects to utilize (at least in a systematic way) biological knowledge i.e. information about ecosystem status, species interactions, and pivotal causal relationships. The goal of this paper was to explore the benefits of incorporating some biological assumptions into an analysis of a precautionary reference point. Specifically, we hypothesized that knowledge of correlation between input variables of SPR would reduce uncertainty of a biological reference point ($F_{30\%SPR}$). The analysis was constructed of two basic elements: (i) fitting the observations of herring growth, maturation, and natural mortality to intrinsic age effects and external environmental effects, and (ii) using these estimates and their possible dependencies in three models to generate a set of SPR curves, when the difference among the models was in the use of biological knowledge.

Material and methods

Herring in the northern Baltic Sea

For Baltic herring, stock assessment and scientific advice are provided by the International Council for the Exploration of the Sea (ICES) and its advisory committee for fisheries management (ACFM). Management measures are determined by the International Baltic Sea Fishery Commission (IBSFC). Herring stocks in the Baltic proper (sub-divisions 25–28) and northern Baltic proper (sub-divisions 29 and 32) are pooled in one assessment unit. This procedure is a compromise between assessment of biologically relevant unit stocks and practical management purposes. As a result, the assessment is uncertain in part due to the complexity of the stock structure in the area (ICES, 1999b). Because herring growth rate varies substantially in different parts of the Baltic (Sjöstrand, 1992; Anon., 1994; Cardinale and Arrhenius, 2000), our simulations apply to the northern Baltic component, and utilize data sampled from ICES subdivisions 29 and 32 (Figure 1).

Weight and maturity data used in the SPR-curve simulations were compiled from database of catch samples routinely collected for stock assessment purposes by Finnish Game and Fisheries Research Institute. Growth data covers period 1974 to 1997 whereas maturity data has been collected since 1982. Parmanne

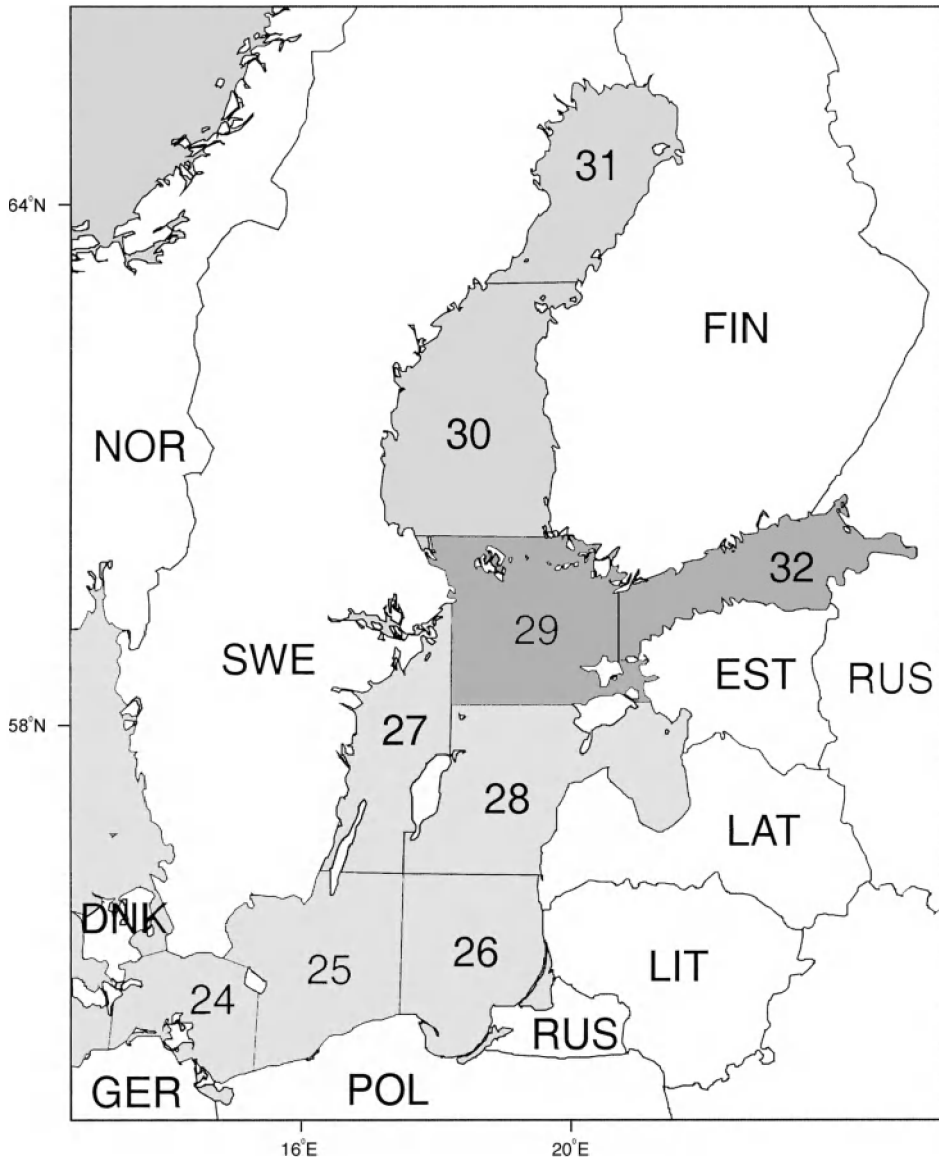


Figure 1. Baltic Sea and the ICES sub-divisions. The ICES herring assessment area for Baltic proper comprises sub-divisions 25–29 and 32. The growth and maturity data is sampled in coastal areas and off shore of Finland (shaded area).

(1990) gives the sampling scheme in detail, but some essential elements of sampling are pointed out here.

The herring maturity data consist of samples taken from commercial trawl landings before the beginning of spawning season. Samples were collected 2 to 5 times annually with each sample including around 100 fish. Sampling was targeted at age-groups 2–4 because in younger ages all herring are immature, and in older ages all are mature. Although the average maturity-at-age has varied substantially, roughly speaking only the minimum and the maximum maturity ogives are statistically different in the time series. This is due to large

variance of estimates and relatively small sample size per age-group.

We considered the first and second quarters of a year as a suitable sampling period for growth analysis. Within that period there is basically no growth increment in herring, although in the otolith of 1-year-old herring some new opaque zone may be visible in June. Weight differences at age were analysed against the quarter of a year (first or second) and gear type (pelagic trawl, bottom trawl, and trap net). No significant differences were found except for age-group one in trap net data against other gear types causing rejection of that

age-group and gear combination from the data set. Trap nets are selective gear for age group one, where only the fastest growing fraction is vulnerable to trap net fishery (Suuronen and Parmanne, 1984). Consequently, data from commercial trawlers and trap nets were pooled for the two first quarters of a year except age-group one.

For the modelling purposes, weight increments – rather than attained weight – were analysed. For a given cohort, growth increment was calculated as the difference between mean weights of successive age-groups. Youngest age considered is age-group one, and the oldest one is twelve.

Estimates of natural mortality were obtained from the Baltic MSVPA (ICES, 1999a), where the natural mortality of herring depends mainly on the biomass of the Baltic cod stock. Large fluctuations in the natural mortality rate paralleled to fluctuations in the cod stock abundance. Although trends in the herring stock dynamics are indisputable in the northern Baltic, estimates of natural mortality and maturity are not precise nor accurate potentially masking correlation between them.

Fitted estimates of maturity, growth rate, and M

Weight increments were parameterized with a two-way ANOVA using year and age-group as additive factors. Weighted GLM-procedure (SAS Institute, 1988) was applied. In the analysis, weighting factor was the inverse of summed variances of weight of fish in the age-groups from which growth increments were calculated. The rationale in using fitted growth increments instead of the observed ones was that growth can be divided into intrinsic age effects and external environmental effects (Weisberg, 1993) to be used in Monte Carlo simulations. The year effects estimate year to year variability in growth rate and characterize changes in the environment, whereas the age effects characterize growth at age for average environmental conditions. Furthermore, the parameters can be estimated taking simultaneously into account both the systematic pattern and error variance in the data. Thus, the “pure” year and age effects of growth increments were estimated. The attained weight-at-age was calculated by summing up weight increments in younger ages (Figure 2).

The linear model assumes additive age and year effects with normal random errors as

$$E(\text{weight increment}_{ij}) = \mu + \alpha_i + \beta_j, \quad (1)$$

where E denotes expected value and μ stands for grand mean. Symbol α denotes age effect at age i and β year effect in year j . Model assumes absolute changes in weight being constant rather than percentage changes. The interaction term is excluded from the model, eliminating systematic changes among main effects.

The same kind of ANOVA was also applied for maturity and natural mortality data. The maturity ogives being percentage values and thus following the binomial distribution were, however, fitted using logit as canonical link function (McCullagh and Nelder, 1989). This model is given by

$$E(\text{maturity}_{ij}) = \exp(\mu + \alpha_i + \beta_j) / [1 + \exp(\mu + \alpha_i + \beta_j)]. \quad (2)$$

After fitting the models, frequency distributions of the year effects were examined using BestFit software (Palisade Corporation, 1993) to find a parametric distribution best matching them. The objective here was to mimic historical variation in growth, maturity, and natural mortality in the simulation trials. We did not consider it appropriate to constrain the range of year effects within the limits estimated by GLM because we feel that if enough time is given to processes in ecosystem the observed range of variables will be exceeded sometime in the future. Instead, we used both the frequency distribution of year effect estimates and our conception of possible future states of ecosystem dynamics to parameterize a theoretical distribution describing environmental effect on the investigated variables. By assuming continuous distributions for year effects, parameter values not yet realized in the data were allowed to occur in Monte Carlo simulations. Concerning the age effects, standard errors of the estimates were transformed to 95% confidence limits under assumption of Gaussian distribution. Thus, stochastic variation within confidence interval was allowed for intrinsic age affects.

SPR analysis

Due to uncertain stock assessment outputs we preferred an approach that did not rely on stock-recruitment information for the SPR analysis. Instead, we utilized conclusions based on a range of worldwide stock assessment results being combined with SPR analysis (Mace and Sissenwine, 1993, table 2). For six Baltic herring stock units included in the analysis, Mace and Sissenwine (1993) estimated that F_{rep} corresponds 18–65% of the virgin biomass SPR. Maximum spawning per recruit (maxSPR) is obtained at fishing mortality rate zero. With increasing fishing intensity, spawning per recruit declines perpetually and can be expressed as percentages of the maximum SPR. As they concluded that a 30% level of SPR is enough for replacement for 80% of all the fish stocks considered, we accepted this as criteria for reference fishing mortality estimate, $F_{30\% \text{SPR}}$.

In contrast to Mace and Sissenwine (1993), we simulated a set of SPR curves instead of developing a single curve, so that the SPR curve was the dynamic element of the analysis. Monte Carlo simulations were carried out utilizing probability distributions estimated for year and age effects of growth, maturity and natural mortality. A

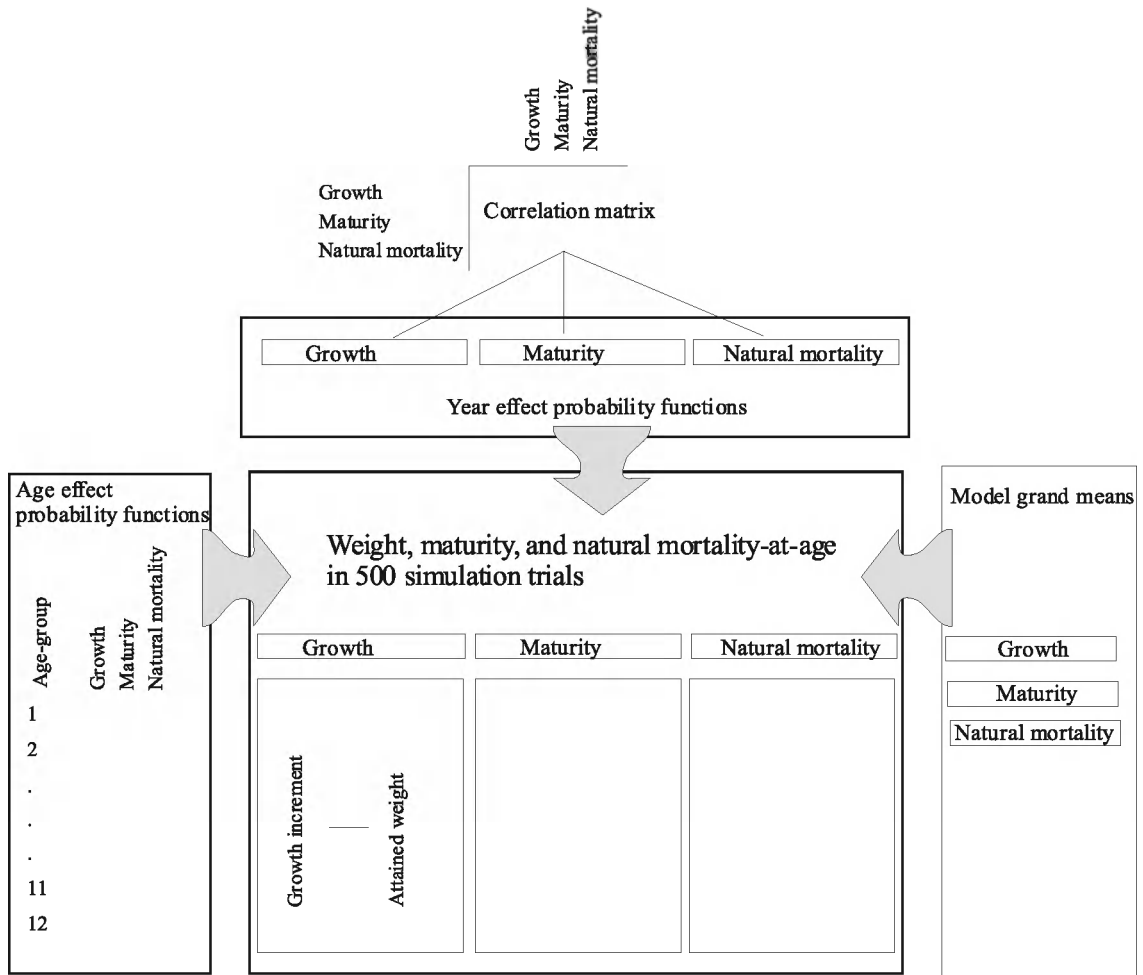


Figure 2. Schematic diagram of Monte Carlo simulations to develop input values for SPR calculations. The strength of causal connections between year effects of input variables are controlled by a correlation matrix. Intrinsic age effects apply for growth, maturity, and natural mortality. Growth is designated as attained mean weight-at-age. SPR inputs from a particular simulation trial are derived as a function of GLM grand means, year effects, and age effects.

conventional age-structured model based on standard population and catch equations was applied (Thompson & Bell, 1934) to calculate SPR curves. Gabriel et al. (1989) give the computational procedure in detail. For convenience, we did not correct our calculations for fraction of mortality before spawning. The selection pattern was assumed fixed and was estimated from the fishing mortality profile in the recent stock assessment (ICES, 1999c).

Three modelling approaches

In addition to exploring the impact of articulated stock dynamics on a biological reference point, our objective was to probe whether utilization of knowledge about causal ecosystem relationships reduces uncertainty of the estimate. The utility of ecological knowledge was

investigated by calculating sets of SPR curves under three different models for input data.

Empirical model

The empirical model is a data oriented approach based strictly on the observed values of weight, maturation, and stock assessment outputs about natural mortality rate during 1974–1997. Input values for SPR calculations were taken from catch samples (growth, maturity ogive) and MSVPA (natural mortality). However, because there were no maturation samples during 1974–1981, average maturity ogives in 1982–1984 were applied for that period. The empirical approach assumed that the future will be precisely like the past. For example, we then must expect that the 24 year monitoring period is long enough to reveal the maximums and minimums of input variables and all their relevant combinations.

Table 1. Correlation coefficients of input variables for SPR curve simulations under the ecological model.

	Growth rate	Maturity	Natural mortality
Growth rate	1		
Maturity	1	1	
Natural mortality	0.9	0.9	1

Furthermore, the stern empirical approach signifies that any theoretical information about mechanisms controlling herring population dynamics is not used to validate results from SPR analysis.

Random model

The random model was constructed under assumption that no correlation among growth, maturity, and natural mortality exists in the herring stock and all their combinations are random. In simulation trials (Figure 2), this was realized by setting the correlation factor to zero between year effects of input variables. Stochastic variation for year and age effects were allowed by appropriate density functions estimated from GLM results. The random model thus included the variance of the input variables but excluded their linkages.

Ecological model

In the ecological model biological and ecological understanding was used. This model assumed complete positive correlation between growth rate and maturation schedule and strong positive correlation between growth rate and natural mortality rate (Table 1). Here, the maturity was assumed to completely depend on attained weight. This is conventional perception among fisheries scientists (e.g. Nikolskii, 1969), even though not applied in the recent assessment (ICES, 2000). The latter interrelation implies that although possible, it is highly unlikely that high natural mortality rate and low growth rate (or vice versa) would simultaneously prevail in the Baltic herring population. In order to accept this view, one should be able to address the mechanism producing this kind of relationship (Figure 3). We suggest, referring to MSVPA results, that cod stock abundance affects herring stock abundance via predation and by creating a major part of the natural mortality (ICES, 1999a, 1999b). To put this in perspective, M has been higher than F during high cod abundance, and when abundant, cod has eaten 1.5 times the amount herring caught by fishermen. Growth rate of herring is in turn linked to herring stock abundance via intraspecies food competition. However, high natural mortality and high stock abundance may occur simultaneously. This is due to the fact that recruitment of cod and herring are not

dependent on each other (ICES, 1999c), and high abundance of herring and cod can materialize simultaneously, at least for a while before predation affects herring abundance. Consequently, complete correlation between growth rate and natural mortality rate is not arguable since there are lags in the ecosystem dynamics.

As for the random model, biological parameters describing growth, maturity, and natural mortality were defined by probability distributions from which combinations of values define a set of input parameters for a particular SPR calculation in Monte Carlo trials. Temporal autocorrelation was not modelled in the simulations.

Defining maximum spawning per recruit

Maximum spawning per recruit, i.e. the virgin SPR, determines SPR of an unfished population. For all three models, model specific maximum SPRs were defined in two ways: (a) as the maximum spawning per recruit for each set of input data, and (b) as the maximum of all input data sets. These values are referred to as annual maxSPR and global maxSPR, respectively. Annual maxSPR can be described as a maximum of any single SPR curve, whereas global maxSPR defines a maximum from a larger set of SPR curves. Global maxSPR is, thus, highly conservative approach. For the empirical model, the estimates of both types of maxSPR are based on the data. Concerning the random and the ecological models, estimates of maxSPR are outcomes from Monte Carlo simulation trials. The global maxSPR was estimated from 1000 simulations prior to simulating the actual output variable, fishing mortality rate corresponding to 30% of maximum SPR, whereas the annual maxSPRs were calculated for each simulated data set. The empirical model has two sets of 24 annual estimates of $F_{30\%SPR}$ based on the observations. Two frequency distributions for $F_{30\%SPR}$ were derived from 500 simulation trials for the random and the ecological models.

The sensitivity analysis was performed on the output variable, $F_{30\%SPR}$, and associated inputs using a multivariate stepwise regression. The regression coefficients are normalized regression coefficients associated with each input. Therefore, a regression value of for instance 1 indicates a 1 standard deviation change in the output for a 1 standard deviation change in the input (Palisade Corporation, 1994).

Results

Estimates of input data and calculation of SPR

The estimated year effects (Table 2) characterize variability in growth rate, maturation, and natural mortality rate during the observed years. R-square in GLM analyses was 0.63 for weight increments, 0.38 for maturity,

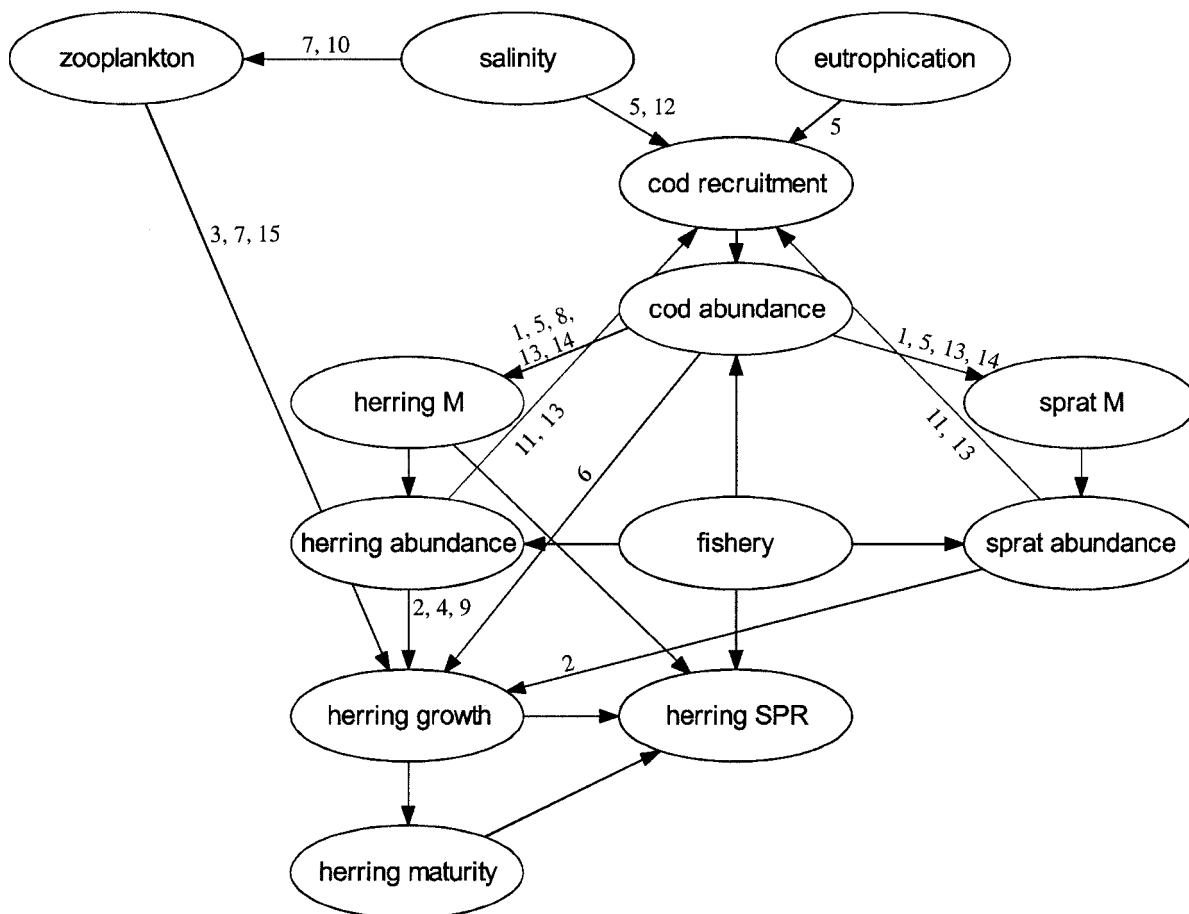


Figure 3. Mechanisms controlling herring stock dynamics and sources of information.

- | | |
|---------------------------------|------------------------------|
| 1 ICES (1999a) | 9 Horbowy (1997) |
| 2 Arrhenius (1995) | 10 Hänninen (1999) |
| 3 Arrhenius and Hansson (1993) | 11 Köster and Schnack (1994) |
| 4 Arrhenius and Hansson (1999) | 12 MacKenzie et al. (1998) |
| 5 Bagge <i>et al.</i> (1994) | 13 Rudstam et al. (1994) |
| 6 Beyer and Lassen (1994) | 14 Sparholt (1994) |
| 7 Flinkman <i>et al.</i> (1998) | 15 Vuorinen et al. (1998) |
| 8 ICES (1999c) | |

and 0.72 for natural mortality rate. The year effect estimates reveal reasonably similar dynamics in growth and natural mortality, the variables having correlation coefficient 0.75 supporting our assumption regarding their linkage (Figure 4). Growth and natural mortality rate have increased from the beginning of the sampling period in the mid-1970s, peaking in the beginning of 1980s, then starting to decline for a decade and even out at the end of time series. This pattern matches with the estimated changes in cod abundance. Growth and maturation year effects do not, however, correlate although a complete correlation was set in the ecological model. The age effects show largest growth increment in age-groups 1 and 2. Maturity ogive increases with age as expected. Natural mortality decreases strongly from age

1 to age 2 and more slowly in older ages (Table 2), for young herring is of suitable size as food items for cod (Sparholt, 1994).

Conventional diagnostics for GLM analysis for growth and maturity data did not demonstrate any conflict between the data and the model. However, mortality data exhibits age*year interaction (Figure 5), which was not included in the model because an interaction term would have saturated the model. As a result of the lack of an interaction term in the model, variability in mortality was estimated to be too small in young ages, and too large in old ages. In simulations this bias was adjusted by allowing larger variation in age effect estimates in age-groups 1–2, and allowing no variation from age-group 3 onwards. The allowed

Table 2. Parameter estimates for year and age effects for growth increment (g year^{-1}), maturity ogive (on logit scale), and natural mortality rate. Year effects apply for period 1974–1996 for growth, 1974–1997 for natural mortality, and 1982–1997 for maturity, respectively. Age effects apply for age-groups 1–12 for growth and natural mortality, and 2–4 for maturity.

Year	Year effects			Age-group	Age effects			Grand mean		
	Growth increment	Natural mortality	Maturity ogive		Growth increment	Natural mortality	Maturity ogive	Growth increment	Natural mortality	Maturity ogive
1974	3.04	0.006		1	6.13	0.278		1.59	0.182	2.08
1975	5.05	0.019		2	2.17	0.078	-3.60			
1976	6.76	0.022		3	0.77	0.058	-0.92			
1977	7.13	0.029		4	0.30	0.038	0.00			
1978	6.66	0.050		5	0.23	0.035				
1979	8.17	0.078		6	1.62	0.022				
1980	9.26	0.081		7	1.26	0.016				
1981	7.72	0.064		8	2.12	0.013				
1982	9.52	0.082	1.14	9	0.10	0.000				
1983	5.01	0.094	1.16	10	0.44	0.000				
1984	3.05	0.055	0.98	11	1.27	0.000				
1985	5.85	0.034	1.48	12	0.00	0.000				
1986	7.60	0.016	1.16							
1987	5.36	0.003	1.24							
1988	5.77	0.011	1.98							
1989	4.13	-0.002	1.46							
1990	-0.41	-0.008	1.97							
1991	1.19	-0.015	2.40							
1992	-0.50	-0.015	1.88							
1993	2.54	-0.012	1.80							
1994	0.97	-0.009	2.08							
1995	-0.19	-0.004	1.67							
1996	0.00	-0.005	1.87							
1997		0.000	0.00							

variation was based on the distribution of residuals by age-group. This has an effect of creating more variation in estimated natural mortality in simulations than allowed by the model itself in the youngest ages. However, variation in simulations in older ages, created solely by the year effects, was still slightly larger than observed variability. This was not considered to be

detrimental to analysis having focus on exploring the dynamics of a biological reference point.

Choosing a theoretical distribution for the estimated year effects to be used in the simulations was to some extent a subjective process. We considered that the distribution should give a good fit to the frequency data and allow for exceeding the observed range of the year effects. Moreover, the distribution should have reasonably similar shape because we assume a strong causality between them. We decided to use the extreme value distribution for natural mortality and growth year effects (Figure 6a and 6c). These distributions did not give a very good fit to the data, but they were the best available. Regarding natural mortality, we assumed we have not faced the minimum nor maximum level of predation in the historical data (Figure 6a). The major part of the probability distribution is located at low natural mortality rates implying that we have a pessimistic perspective concerning the rebuilding of the cod stock during current management regime and stagnation phase in Baltic Sea. On the contrary, it is possible, but not likely that natural mortality will exceed the historical level in the future. The same reasoning applies also for the distribution simulating the growth year effects. Based on the empirical data, the uniform distribution

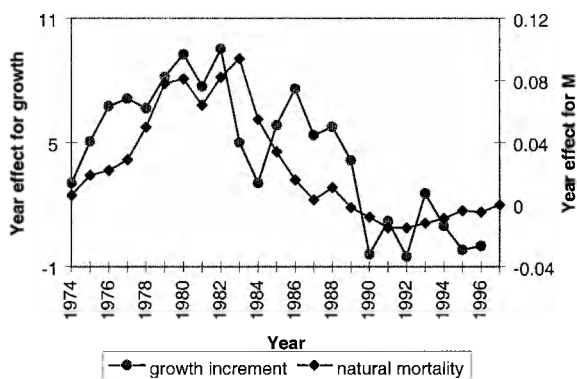


Figure 4. Year effect estimates for growth increment and natural mortality data from additive model for period 1974–1996.

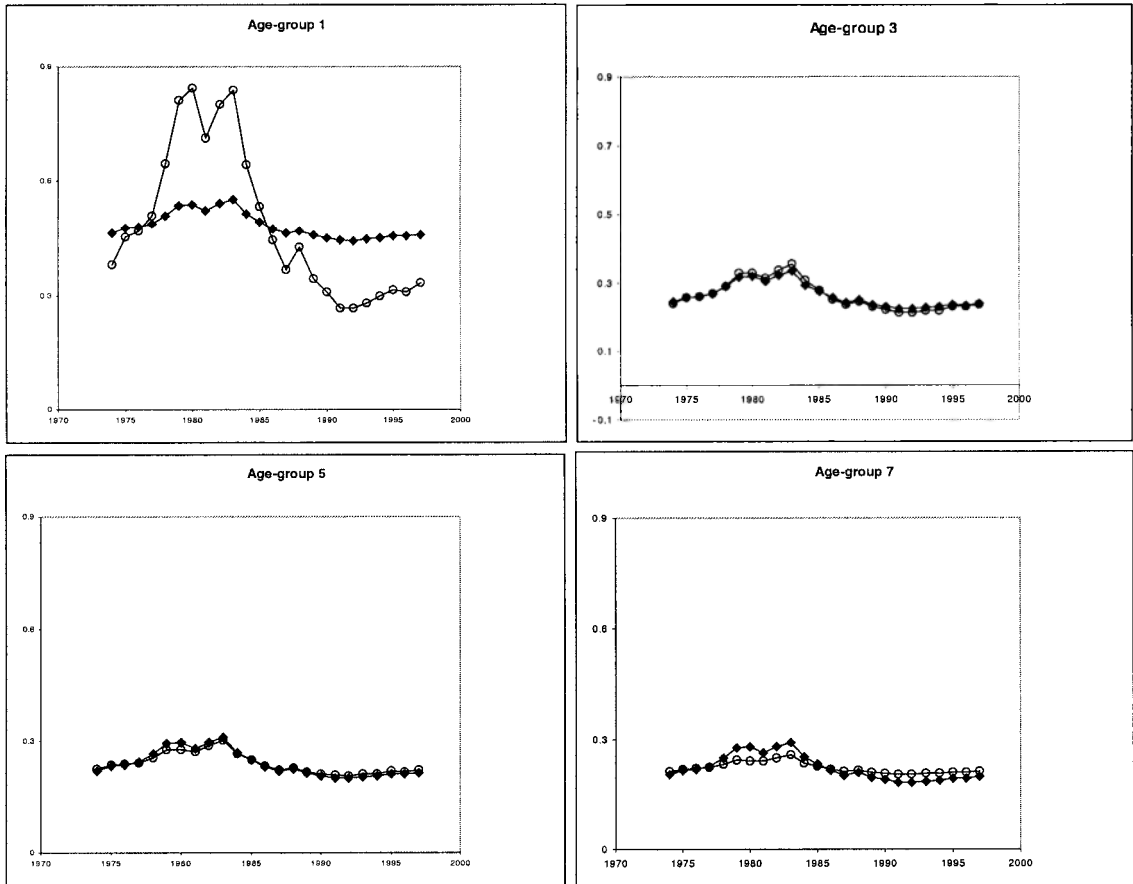


Figure 5. Observed (—○—) and predicted (—◆—) natural mortality rates in age-groups 1, 3, 5, and 7. The model underestimates variability in age-groups 1 and 2, does reasonably well in ages 3–6, and overestimates variability from age-group 7 onwards.

would seem to be justified, but this would not allow for exceeding the observed range. We nevertheless relied more on our theoretical understanding and chose the extreme value distribution (Figure 6c). Also this distribution is skewed to the right implying we are assuming that slow growth of herring is more likely in the future than it has been in the past. For maturation we chose the Weibull distribution (Figure 6b). The criteria here was solely the fit to the data.

The simulated input data for SPR calculations including weight, maturity, and natural mortality-at-age has the pattern of observed values but larger variability created by the probability functions used. In the raw data there are several negative weight increments which can be either artifacts caused by unrepresentative sampling or ageing errors, or may be valid observations from the population. This latter explanation is quite possible, since during the growth degradation the condition factor of herring has decreased. We hence allowed negative weight increments also in the simulations.

Reference fishing mortality rate under three model approaches

The global maxSPR was 0.14 kg/recruit in the empirical model. In the simulations, the global maxSPR varied from 0.31 (kg/recruit) for the random model to 0.20 (kg/recruit) for the ecological model. This variation turned out to be significant regarding $F_{30\%SPR}$ estimates for the three models explored. The probability distributions of $F_{30\%SPR}$ were fundamentally different depending on derivation of maxSPR (the vertical panels of Figure 7), but also the applied model impacted the results (the horizontal panels of Figure 7). Because the reference fishing mortality rate is defined as a fraction of maximum spawning per recruit, maxSPR acts as a scaling factor affecting the distribution of the estimates. When global maxSPR was applied, high maxSPR caused $F_{30\%SPR}$ estimates to concentrate near the origin, whereas lower maxSPR was connected with higher reference fishing mortality (Figure 7a, b, c). Using

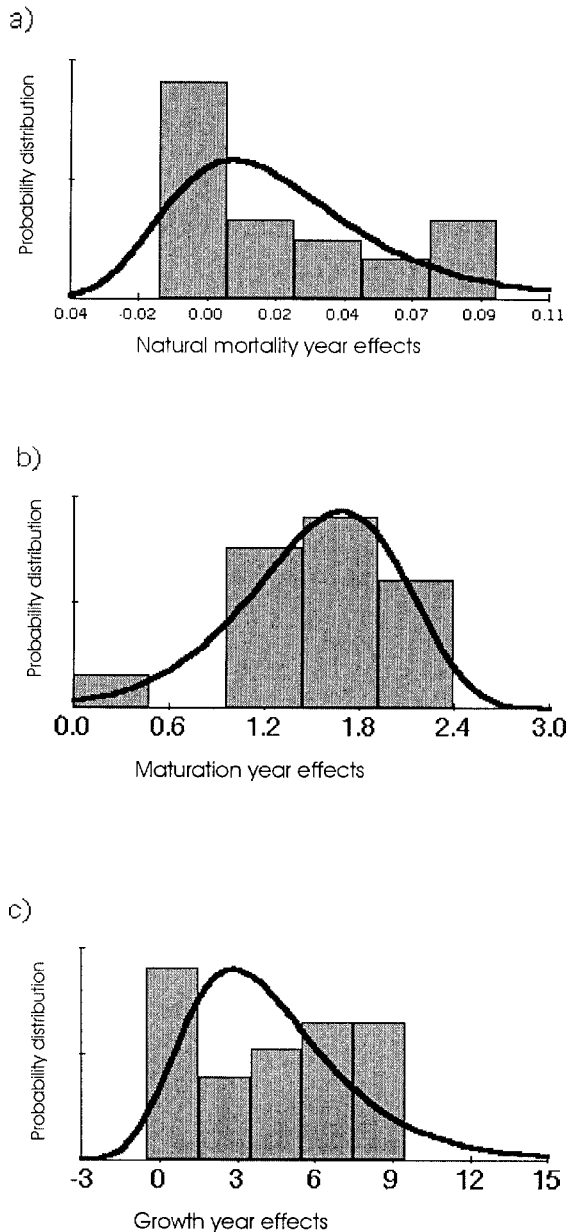


Figure 6. Frequency distributions for natural mortality (a), maturity (b), and growth (c) year effects (bars) with eligible theoretical distribution (curve) for Monte Carlo simulation trials.

annual maxSPR resulted in markedly higher $F_{30\%SPR}$ estimates (Figure 7d, e, f) than using global maxSPR.

We first focus on results derived with global maxSPR. The probability distribution of $F_{30\%SPR}$ for the empirical model was reasonably uniform in the range of 0.09–0.45 (Figure 7a) reflecting change in BRP when environment (growth and mortality) has fluctuated back and forth between low and high state. The empirical

model is, thus, a fairly uninformative basis for management advice. The random model has the most aberrant $F_{30\%SPR}$ distribution, where the majority of reference fishing mortalities lie between 0.00 and 0.05 implying that in practice no fishing should be allowed in order to conserve the stock (Figure 7b). Relatively low $F_{30\%SPR}$ rates are suggested also by the ecological model. Here, the stock is estimated to withstand fishing mortality rates 0.06–0.20 (Figure 7c) under the majority of input disturbances. The three models result in different management advice and demonstrate the significant structural uncertainty in addition to the parameter uncertainty shown by the wide range of the $F_{30\%SPR}$ distributions.

Reference fishing mortality rates increased markedly and the shape of their distribution changed in all three models when annual maxSPR was used instead of global maxSPR. Variability in BRP estimates was considerably smaller in the empirical model (Figure 7d), but generally remained at and above the upper bound of outcome with global maxSPR. The $F_{30\%SPR}$ distributions of the random and the ecological models were very similar to each other (Figure 7e and 7f) basically reflecting the parametric distributions of input variables used for resampling in simulation trials. Medians of $F_{30\%SPR}$ estimates were identical in practice (0.37 in the ecological model and 0.38 in the random model). The overall within model variability was large in both models the range being 0.25–0.65. The usefulness of ecological causal knowledge in reducing uncertainty about BRP estimates may be judged from the distributions in Figure 7e and 7f. The only difference which has affected these model outcomes is the level of correlation between the input variables in Monte Carlo simulations (Table 1). Although the cumulative probability distribution of the ecological model has slightly shorter tails than the random model (Figure 8), indicating that causal biological information has decreased uncertainty, it can not be argued that this information has any pragmatic surplus value in the studied case despite the fact that these distributions are statistically different ($\chi^2=75.8$, prob. <0.01).

Use of biological information in the “ecological model” resulted in little reduction in uncertainty and result in an insignificant improvement in giving scientific management advice. It is, however, obvious that outcomes from both random and ecological models call for more cautious management advice than would be the case if based on historical data only. This important conclusion is valid with all derivations of maxSPR.

The output from sensitivity analysis was different depending on the definition of maxSPR. None of the year or age effects had notable impact on $F_{30\%SPR}$ when annual maxSPR was applied, whereas year effects in special had significant consequence on the BRP when global maxSPR was used. The explanation for lack of

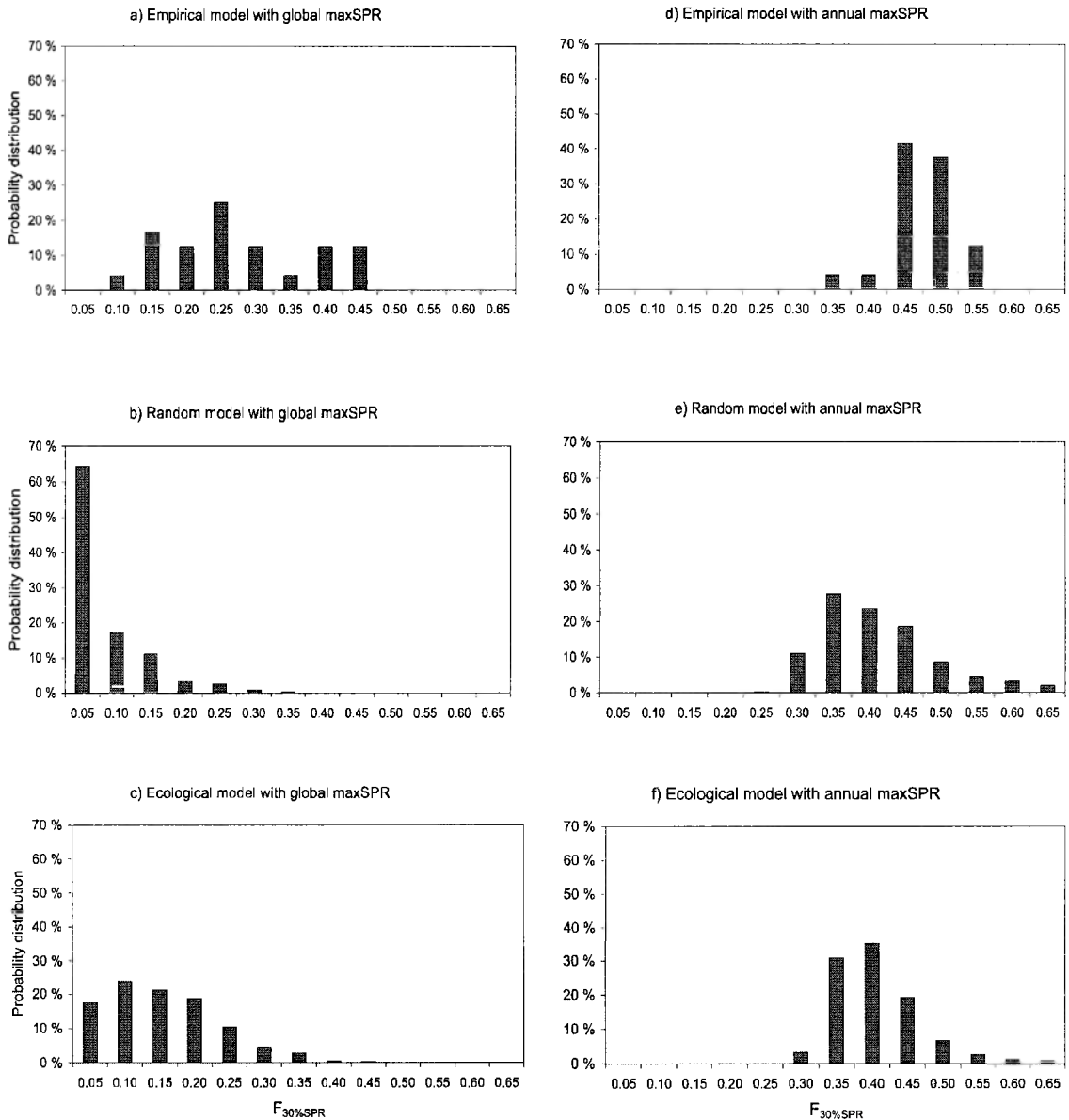


Figure 7. Probability distribution of estimated $F_{30\%SPR}$ for all models (see text for further information). The values on x-axis represent the upper bound of the class.

any effect of variability in growth, maturation or natural mortality on the $F_{30\%SPR}$ in affiliation with annual maxSPR is that this biological reference point is defined as a constant fraction of SPR with no fishing. SPR curves were “internally scaled” in simulation trials in the sense that input parameters have affected more strongly the level than shape of the curve. As a consequence, variance in growth, maturation and natural mortality has not had significant effect on fishing mortality corresponding to 30% of maximum spawning per recruit. However,

this result does not imply stability of the BPR and the simulated distributions were wide (Figure 7e and 7f).

Year effect estimates became significant in the random and the ecological models using global maxSPR (Figure 9). In both models the growth year effect has dominated simulation results. The linkage between annual growth rate (growth year effect) and $F_{30\%SPR}$ is positive indicating that resilience of herring stock is presumed to increase along growth rate. The negative relationship between annual natural mortality rate (M year effect)

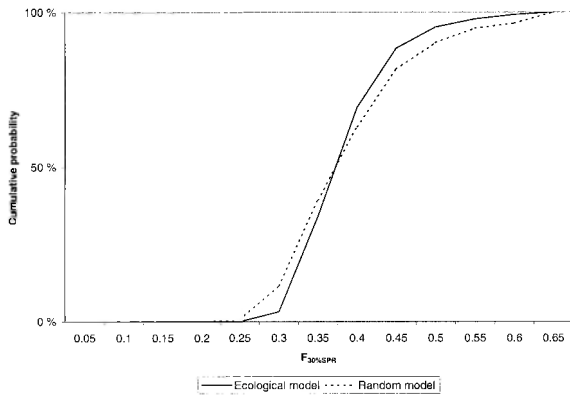


Figure 8. Cumulative probability distribution of the reference fishing mortality rates for the random and the ecological models using annual maxSPR.

and $F_{30\%SPR}$ indicates that during periods of high M , caused by high abundance of the predator, cod, the resilience of herring stock is presumed to decrease. The direction of correlation between $F_{30\%SPR}$ and growth and natural mortality imply that when reference fishing mortality rate is defined according to global maxSPR, this biological reference point tends to stabilize stock size and does not act as a ratio reference point. Growth and natural mortality year effects have a reverse effect on the spawning-per-recruit and hence on reference fishing mortality rate. A strong positive correlation has been set between these year effects in the ecological model (Table 1) in part canceling out their effects on $F_{30\%SPR}$. This is a possible explanation for the exiguous impact of the biological knowledge applied in the ecological model on the distribution of reference fishing mortality. Unfortunately, the degree of correlation in the herring stock between growth and natural mortality is hard to predict, for there are time lags in the population reactions to changing ecosystem factors (e.g. predator abundance). In addition, age effects in age-group one on natural mortality and growth impacted the model outcomes evidently, but much less than growth and M year effects.

The difference that biological knowledge makes in the two simulation models deals with the effect of maturity year effect. In the random model maturity year effect has a minor impact on $F_{30\%SPR}$ whereas the impact is substantially larger in the ecological model. This observation points out that biological information concerning relationship between growth rate and maturation is potentially relevant with respect the studies connected to resilience.

Discussion

We applied an array of modelling approaches to a herring stock as a case study in calculating spawning

per recruit, and to examine whether ecological causal knowledge reduces uncertainty of a BRP estimate. Derivation of maxSPR appeared to have the greatest impact on the location of reference point estimates and also the within model variation. Estimates of $F_{30\%SPR}$ were influenced also by the model used (assumed causal connections), although results are to some extent confounded by the definition and criteria for maxSPR and BRP. The parameter uncertainty, caused by a highly dynamic stock, was of importance with respect to management advice. The results suggest that using only the observed data leads more likely to overestimation of the resilience than using simulated data and, thus, is a risky approach in stock assessment. Several arguments support using simple but theoretically justified assumptions of the characteristics and strength of the relationship between growth, maturity and natural mortality of herring:

- (i) In a scale of long term ecosystem variability, fisheries data for Baltic herring are available only for a limited temporal range to quantify the population's response to environmental factors, although the range in growth rate and natural mortality rate have been large. As a result, part of the relevant input variable combinations are likely to be absent in the data. The lack of historical perspective means that the knowledge of natural variability of fish population parameters is uncertain. In the terms of conventional statistics our perception of ecological processes may be biased due to unrepresentative sampling from possible ecosystem statuses ("empty cells" in data). Taking the ecosystem approach is essential to take into account the possibility of the simultaneous occurrence of the unfavourable state of input variables. This is of importance in making risk assessment of exceeding biologically safe harvesting rate.
- (ii) Modelling ecological linkages points out how they influence the outcome and the information content of the SPR analysis. This addresses areas requiring further research and encourages formulation of explicit hypothesis regarding relevant biotic and abiotic ecosystem processes. According to sensitivity analysis, processes affecting growth and natural mortality are of about equal significance. However, mechanisms controlling natural mortality are thought to be better understood than mechanisms controlling growth.
- (iii) Multispecies interactions are significant in the Baltic ecosystem and must be analyzed with respect to management advice. Single species models are in danger of giving wrong answers and therefore tools capable of embracing multispecies assessment and management issues are needed.

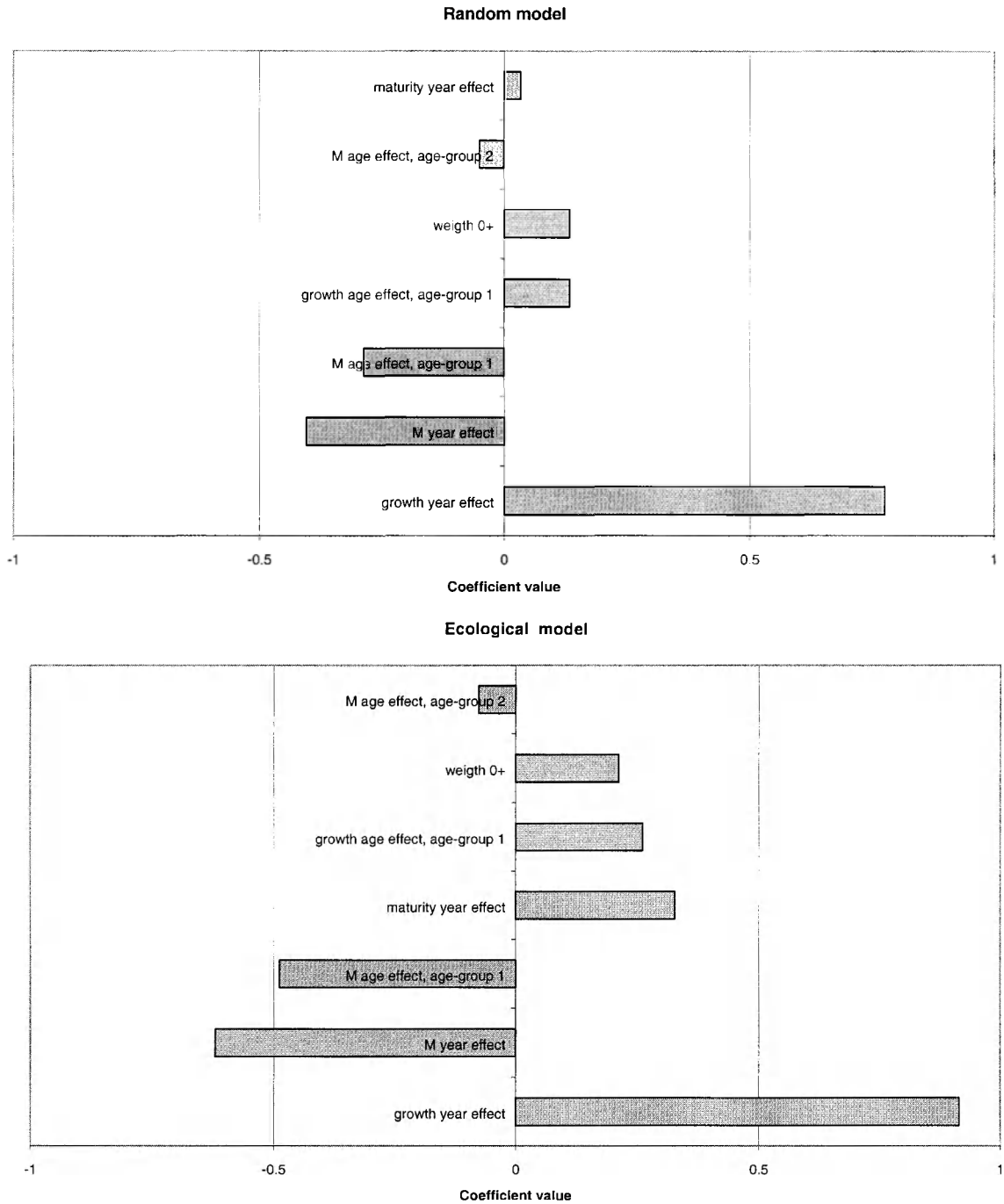


Figure 9. Sensitivity analysis for input parameters in random and ecological models.

Results imply that when SPR analysis is based on only very few years of data the risk of grossly over-estimating stock resilience is high. This phenomenon should be considered when dealing with highly dynamic stocks like Baltic herring and with very small data sets. The bias is likely not as significant among

stocks with more stable growth and natural mortality rates.

Maximum SPR, also referred to as virgin stock spawning per recruit, may be estimated without any confusion for a fish population having considerable stability in life history parameters. For these stocks

maxSPR can be interpreted on stock-recruitment scale assuming assessment outputs are available. When virgin spawning biomass and corresponding recruitment are obtainable they help validating whether estimated maxSPR is meaningful. This procedure is comparable to our “annual maxSPR” approach in the way that maxSPR is defined, but differ in that we have developed several SPR curves and we are lacking accurate stock assessment outputs for the analyzed stock component. It is worth pondering whether the wide range of $F_{30\%SPR}$ estimates observed in all models indicate true changes in resilience and, consequently, the need to change BRP when environment change, or whether it mostly indicates uncertainty of the estimate. [Rochet \(2000\)](#) has demonstrated that density dependent mechanisms in the adult population (e.g. growth rate, maturation schedule, fecundity, and egg size) may break down the proportionality between spawning stock biomass and recruitment making spawning per recruit an ambiguous concept. In addition, potential confounding in defining maximum SPR makes spawning per recruit analysis dubious. The difficulty is obtaining a reliable estimate of virgin SPR due to large variation in growth and natural mortality, and in special due to uncertainty about their linkage to stock abundance and to possible density dependent processes in Baltic herring.

If unambiguous conceptual definition and small uncertainty of a reference point are accepted as criteria of usefulness, $F_{x\%SPR}$ does not seem to be a warranted biological reference point for any highly dynamic fish stock. It must, nevertheless, be realized that reference points are not fixed values, although this may be a tempting attribute from management standpoint. The magnitude of variability inherent in the reference point and consequent management advice displayed by all used models would be hard to accept by a fisheries manager and fishing industry. Reference points should, however, depend on the true changes in environment, and would be expected to change in parallel with regime shifts in the ecosystem.

The reference point used here is inevitably arbitrary, defined as 30% of maximum SPR. Moreover, we have used spawning stock biomass as a proxy for egg production excluding all other fish biological interactions potentially affecting reproducing success. Substantial changes in herring weight-at-age may have affected selectivity, but this effect has been omitted from SPR calculations. A parameterized selectivity model would have been available ([Suuronen, 1995](#)), and changes in selectivity could have been incorporated easily in calculations of spawning per recruit. However, prospectively high escapement mortality ([Suuronen et al., 1996](#)) would have compelled more assumptions in the analysis. Adjustments for selectivity were judged to have been unnecessary embellishment of the model. Due to these factors the calculated BRP can not be regarded as an

estimate of true resilience of the stock; it was basically used to obtain comparable results among the models.

Model uncertainty can be divided into parameter uncertainty and structural uncertainty ([Punt and Hilborn, 1997](#)). Structural uncertainty signifies that the processes of interest can be described by several models, which may have different outcomes in conjunction with essential scientific conclusions or practical decision making. With respect to fisheries management, the parameter uncertainty is in many cases of less importance than the structural uncertainty ([Punt and Hilborn, 1997](#); [Francis and Shotton, 1997](#); [Kuikka, 1998](#); [Kuikka et al., 1999](#)). Parameter uncertainty of a reference point was investigated as a function of varying growth, maturity, and natural mortality under different assumptions about causal relationships between these variables addressing structural uncertainty. As a part of the management process, this can be defined as risk assessment according to concept suggested by [Lane and Stephenson \(1998\)](#).

The approach by the ICES Baltic fisheries assessment working group has currently strong elements of the empirical and random modelling. For example, in subdivisions 25–29 and 32, maturity at age has so far been assumed constant by the assessment working group ([ICES, 2000](#)), suggestive of random modelling. Thus, possible decline in maturity connected with growth degradation has not been reflected in estimates of spawning stock biomass, potentially affecting all calculations using maturation as input data including stock-recruitment relationship, SPR analysis, and biological reference points.

There is evidently a need for better biological basis for scientific advice and management approach concerning Baltic herring, including issues of basic research: factors controlling growth of herring and interaction between growth, fecundity, and viability of eggs. Fisheries management is challenged in face with uncertainty of current and future causal relationships in the ecosystem. Clearly, assessment and management must be linked to broader ecosystem state. If growth degradation is caused by limited access to food items (neritic zooplankton), mechanical implementation of precautionary approach and restrictive management may implicate risking population growth rate, reproduction capacity, and resilience. On the other hand, knowledge is lacking whether growth rate would be better in lower herring stock abundance, caused by intensive fishing. At this point, modelling can be used as a decision analysis tool which permits use of ecological and fisheries information in comparing large scale and long-term management options.

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