



MSY-orientated management of Baltic Sea herring (*Clupea harengus*) during different ecosystem regimes

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The Baltic Sea ecosystem has undergone dramatic changes, so-called ecosystem regime shifts, during the past four decades. Baltic Sea herring (*Clupea harengus*) spawning-stock biomass has declined to a third, and weight-at-age has halved as a result of food shortages and competition with sprat (*Sprattus sprattus*). The management objective for the herring stock is currently in transition from pre-cautionary to maximum sustainable yield (MSY). The main basin Baltic Sea herring was modelled under the current ecosystem regime and the effect of a recovery of the cod (*Gadus morhua*) stock and the availability of planktonic food to levels found in the early 1980s analysed. A target of $F_{\text{MSY}} = 0.16$ for herring, which should decline to $F_{\text{MSY}} = 0.10$ with recovery of the cod stock, is proposed. An increase in the availability of planktonic food is estimated to more than double the yield at $F_{\text{MSY}} = 0.27$, overriding the negative effects of cod predation should there be a simultaneous increase in both cod and availability of planktonic food. The estimated net increase in yield is 40% at $F_{\text{MSY}} = 0.20$. Functions are presented to calculate F_{MSY} and to estimate the expected yield depending on the abundance of cod and food availability. Retrospective application of the functions is indicative of overfishing of herring in the 1990s and early 2000s, and a net loss in yield, with a landing value of some €440 million.

Keywords: density-dependence, fishing mortality, productivity, sustainability, weight-at-age, yield.

Introduction

The decline in weight-at-age of the Baltic Sea subspecies of Atlantic herring (*Clupea harengus membras*) in Baltic Sea catches has been notable. From the early 1980s to the mid-1990s, the average weight-at-age halved, and since then it has only recovered partially (ICES, 2010). Evidence points towards food shortage as the underlying cause. The quantity of food in herring stomachs and the mesenteric fat storage dropped between samples taken in 1991 and those collected in 1986, despite an increase in total plankton biomass in the Baltic Sea (Flinkman *et al.*, 1998). The reason hypothesized for the decline is the decrease in the abundance of the most important prey species, the copepod *Pseudocalanus* sp., during the main period of herring growth in spring and summer (Möllmann *et al.*, 2003, 2008; Rönkkönen *et al.*, 2004). In autumn and winter, the diet is broader, medium-sized and large herring feeding on mysids too (Möllmann *et al.*, 2004). The fecundity of *Pseudocalanus* sp. has been suggested to depend on a relatively high deep-water salinity compared with prevalent Baltic Sea conditions (Möllmann and Köster, 2002; Renz and Hirche, 2006). Baltic Sea deep-water salinity is controlled by the major inflow of North Sea water through the Danish straits,

hypothesized to be controlled by the North Atlantic Oscillation (Hänninen *et al.*, 2000). Bottom-up control of herring body growth by salinity, via *Pseudocalanus* availability, has consequently been proposed in several studies (Flinkman *et al.*, 1998; Rönkkönen *et al.*, 2004). Other studies support the notion that food competition with sprat (*Sprattus sprattus*) during spring is responsible for the decrease in body mass (BM) in herring (Möllmann *et al.*, 2004; Casini *et al.*, 2006).

It is probable that both the salinity-induced decline in food availability and increased competition with sprat have had an effect on herring growth (Möllmann *et al.*, 2005), although food competition with sprat has likely had an overriding effect at high densities of sprat (Casini *et al.*, 2010). The changes in the Baltic Sea ecosystem have been so substantial that it has been proposed that the Sea underwent a possibly irreversible ecosystem regime shift in the late 1980s/early 1990s (Österblom *et al.*, 2007; Möllmann *et al.*, 2008). The recent regime shift raises the spectre of modified or impaired ecosystem services of the Baltic Sea, e.g. the production of fish for human consumption and feed. For the Baltic Sea herring, the decline in weight-at-age may be associated with lower stock productivity, because smaller females potentially

produce fewer eggs (Óskarsson and Taggart, 2006) and eggs from leaner females are less likely to hatch (Laine and Rajasilta, 1999).

ICES has, since 2002, proposed that the herring stock in the Baltic Sea main basin be exploited at a precautionary level of $F_{pa} = 0.19$ (ICES, 2009a). Recently too, the European Commission requested ICES to explore the possibility of applying a fishing mortality (F) based on maximum sustainable yield (MSY), taking into account the implications of an increased cod stock (ICES, 2009b). Further, they asked ICES to evaluate the ecosystem effects of a reduction in the size of the sprat stock as a consequence of increased fishing, and ICES developed guidelines on how to implement an F_{MSY} framework (ICES, 2011). If a full management plan does not exist, exploitation targets need to be based on the evaluation of stochastic population models and their errors (ICES, 2011, p. 20), but until now, stock models have not been developed and analysed for that purpose.

To meet the recent demands in the transition to MSY-orientated management, we constructed a population dynamics model of herring in the Baltic Sea main basin. The model is based on statistical analyses of intraspecific density-dependence and the impact of sprat and cod stock sizes on population-growth parameters. Productivity is quantified in terms of MSY and the associated F_{MSY} for four scenarios: (i) before the regime shift, with a large cod stock and good food availability for herring, (ii) the current situation with a small cod stock and poor food availability, (iii) a future with an enlarged cod stock, and (iv) increased food availability (e.g. with a decreased sprat stock and changes in large-scale hydrographic conditions). The forecast developments in weight-at-age and spawning-stock biomass (SSB) are also derived.

Methods

Model overview

A population dynamics model for the herring stock in the main basin of the Baltic Sea to be used for MSY simulation analyses was constructed. Population dynamics need to incorporate negative feedback for growth, for a maximum to exist in the yield function. Negative feedback can be modelled in two ways: via density-dependent recruitment or survival as in surplus production models, or density-dependent individual growth as in yield-per-recruit models (Jennings *et al.*, 2001). Both types of negative feedback are important, because they directly affect the yield that can be harvested sustainably. In addition, we looked at the impact of three variables, cod biomass, sprat biomass, and salinity, on the MSY-related targets.

The herring biomass stock model has the following form:

$$N_{a,y+1} = \begin{cases} R_y, & a = 1 \\ N_{a-1,y} \exp(-Z_{a-1,y}), & a = 2, \dots, 7, \\ N_{a-1,y} \exp(-Z_{a-1,y}) + N_{a,y} \exp(-Z_{a,y}), & a = 8+ \end{cases} \quad (1)$$

$$\bar{W}_{a,y+1} = \begin{cases} \bar{W}_{1,y}, & a = 1 \\ \bar{W}_{a-1,y} + G_{a-1,y}, & a = 2, \dots, 7, \\ \frac{(\bar{W}_{a-1,y} + G_{a-1,y})N_{a-1,y} \exp(-Z_{a-1,y}) + (\bar{W}_{a,y} + G_{a,y})N_{a,y} \exp(-Z_{a,y})}{N_{a-1,y} \exp(-Z_{a-1,y}) + N_{a,y} \exp(-Z_{a,y})}, & a = 8+ \end{cases} \quad (2)$$

where $N_{a,y}$ are the numbers at age a in year y , and $\bar{W}_{a,y}$ is the average weight-at-age on 1 January. The model has four types of transition functions that determine (i) the number of recruits, R_y , (ii) the total mortality, $Z_{a,y}$, (iii) the average weight of recruits, $\bar{W}_{1,y}$, and (iv) the average body growth, $G_{a,y}$. The parameters of the transition functions were estimated using input data and outputs from ICES stock assessments (ICES, 2009a), using herring weight-at-age data for the years 1974–2007 in the Baltic Sea main basin (Subdivisions 25–27, 28.2, 29, and 32; ICES, 2009a). Estimated numbers-at-age $N_{y,a}$, SSB, and natural mortality $M_{a,y}$ were taken from extended survivor analyses (ICES, 2009a). For statistical estimates of transition function population parameters, we employed general linear models using STATISTICA (StatSoft Inc.). The sums of squares of the error in the ANOVA tables were used as the variance for the random errors added to R_y , $Z_{a,y}$, $\bar{W}_{1,y}$, and $G_{a,y}$ in stochastic model simulations.

Mortality function

To separate intraspecific density-dependent natural mortality from cod predation mortality, a linear multiple regression model was fitted to annual mortality $M_{a,y}$ estimates from ICES (2009a):

$$M_{a,y} = m_a + \sum_j \alpha_{a,j} N_{j,y} + \nu_a C_y + \varepsilon_y, \quad (3)$$

where m_a is the age-specific baseline mortality, $\alpha_{a,j}$ the density-dependent mortality effects of age class j on age class a , and ν_a is the parameter for the predation in relation to total cod biomass C_y in year y . A value of $\alpha_{a,j}$ different from zero would demonstrate density-dependence. Total mortality is $Z_{a,y} = M_{a,y} + F_{a,y}$, where $F_{a,y}$ is the fishing mortality. The yield from fishing $\gamma_{a,y}$ is calculated using Baranov's catch equation:

$$\gamma_{a,y} = N_{a,y} \frac{F_{a,y}}{F_{a,y} + M_{a,y}} (1 - \exp(-F_{a,y} - M_{a,y})). \quad (4)$$

Recruitment function

The selection of a recruits-per-spawning-stock (R – S) function is generally difficult, because most juvenile fish undergo several ontogenic stages with different mortality agents (Walters and Martell, 2004). We selected the quadratic function

$$R_{y+1} = \text{SSB}_y (b + d \text{SSB}_y + \varepsilon_y), \quad (5)$$

then linearized it by making recruits per SSB the dependent variable. This function is closely related to the more commonly employed R – S functions (Lassen and Medley, 2000). The quadratic equation can be derived from the mechanics of interactions: negative effects appear as a cause of two individuals being within a specified distance from each other (assuming that the population is spread randomly). Calculations of age-specific SSB partial (0.3) mortality and increase in weight before reproduction:

$$\text{SSB}_{a,y} = (\bar{w}_{a,y} + 0.3G_{a,y})N_{a,y} \exp(-0.3Z_{a,y}), \quad (6)$$

which is summed over age taking into account the maturity ogive of 70 and 90% for 2- and 3-year olds, respectively (ICES, 2010), to obtain total SSB.

Growth function

We fitted a von Bertalanffy model, with growth a negative function of average weight-at-age. To account for growth depending on salinity or food competition with sprat (see above), a growth-year effect, which is common for all herring cohorts, was added. The year effect is later explained by multiple regression with salinity, and sprat and herring densities. The von Bertalanffy model is believed to apply to reproducing individuals only (Lester *et al.*, 2004), so age was included as a categorical variable to account for the proportion of non-reproductive individuals in younger age classes. The model for body growth, $G_{a,y}$, is then

$$G_{a,y} = c + k_y + k_a + l\bar{W}_{a,y} + \varepsilon_{a,y}, \quad (7)$$

in which c is a constant, k_y the year effect, k_a the age effect, l the weight-effect parameter, and $\varepsilon_{a,y}$ the unexplained variation.

Estimating the body mass of 1-year olds

An analysis of the impact of biomass of herring age classes on the biomass of 1-year-old herring the year after, exhibiting positive correlations for the older age classes and negative correlations for the younger ones, was carried out (Supplementary material). There was no significant effect of sprat biomass (Supplementary material), suggesting that there is no consistent effect of competition from older age classes influencing the weight of 1-year olds. Rather, this pattern could be the result of a parental effect on offspring weight: i.e. the weight of recruits is positively correlated with parental age and weight, for which there is some evidence (Blaxter and Hempel, 1963; Morley *et al.*, 1999; Geffen, 2009). We therefore used average parental weight as a linear predictor of $\bar{W}_{1,y}$ by accounting for the age and average weight of their mothers:

$$\bar{W}_{1,y+1} = m + k \frac{\sum_{a>1} (N_{1,y}^a \bar{W}_{y,a})}{\sum_{a>1} N_{1,y}^a} + \varepsilon_y, \quad (8)$$

where $N_{1,y}^a$ is the number of 1-year olds from mothers aged a , m the intercept of the regression, and k a proportionality constant. The number of recruits $N_{1,y}^a$ per female age class was calculated using the age-class-specific SSB from the recruitment function [Equation (5)].

Environmental conditions

The stock model has two environmental variables that affect the herring population: cod SSB [C , Equation (3)] and the year effect for herring body growth, year growth [k_y , Equation (7)]. The latter represents the combined effects of salinity and competition with sprat. They potentially constitute the environmental elements that are part of the regime shift in the Baltic Sea. Fourier analysis was performed on these variables to distinguish long-term interannually correlated changes from random uncorrelated interannual variation, to characterize the regime shift. The Fourier model is

$$y = a + \sum_i (b_i \cos(f_i x) + c_i \sin(f_i x)), \quad (9)$$

where y is the environmental variable, f_i the frequency, x the year, and a , b_i and c_i the parameters, the last being frequency-specific amplitudes. In a spectral analysis, we identified the long

frequencies with the highest spectral densities, then indexed them and used them in Equation (9), with year growth and cod SSB as dependent variables, and year the explanatory variable (fitted in STATISTICA®). The unexplained variation was taken as the estimate of random interannual variation in cod SSB and year growth. In the simulations, the environmental variables were controlled, but a random value from the distribution of the interannual variation was added to historical or forecast values at each iterated year step.

Year growth was correlated with total sprat biomass, total herring biomass, total numbers of herring, and salinity data from 1974 to 2007, obtained from the Swedish Meteorological and Hydrological Institute (SMHI). Data on salinity by depth and month from stations BY10 (southeast Gotland basin), BY15 (east Gotland basin), BY20 (Fårö basin), BY29 (northeast Gotland basin), BY31 (Landsort basin), BY32 (Norrköping basin), and BY38 (Karlsö basin) were used. The salinity data were categorized in three ways: by station, by depth (0, 20, 70, and >70 m), and by quarter. For each categorization, the data were averaged in terms of the other two parameters. To reduce the number of salinity dataseries, we selected station, depth, and quarter with the highest Pearson correlation with year growth and looked for breakpoints in the correlations with sprat abundance, as reported by Casini *et al.* (2010). As a result, the data were categorized with regard to a total sprat abundance breakpoint of 18×10^{10} individuals.

Estimating F_{MSY}

To investigate the productivity of the herring population before and after the regime shift, Monte Carlo (MC) simulations of the population model were run with the averages of the environmental parameters for the periods 1974–1987 and 1990–2007. Fishing was simulated with constant F over 40 000 years to average out longlasting effects of stochastic perturbations and recorded the average annual yield and standard deviation (s.d.) over the past 39 500 years (to move away from initial conditions). Simulations are repeated for F ranging from 0 to 0.5 in steps of 0.01 to identify the value of F that would provide MSY.

Scenario modelling

Four scenarios were simulated, based on the long-term changes determined through Fourier analyses of historical data: (i) unchanged external variables, (ii) a linear increase in cod SSB at the maximum historical rate up to a maximum value, after which it remains constant, (iii) a linear increase in year growth with a maximum historical rate up to the maximum value, after which it remains constant, and (iv) simultaneous increase in both cod SSB and year growth, as in (ii) and (iii). The herring population variables weight-at-age and numbers-at-age were initiated with ICES 2007 estimates. F was modified annually to take into account changes in the external variables and their effect on MSY [see Equation (10) for detail]. The forecasts were 30-year projections starting in 2008. The random interannual variation estimated above was added to the environmental variables. The runs were repeated 100 times to capture the stochastic behaviour of the population and the variability in environmental conditions.

Results

Recruitment, mortality, and growth estimates

Estimates of natural mortality through cod predation differed significantly between ages and with cod biomass (Table 1). There was poor and ambiguous evidence of density-dependence between herring age classes (Table 1). Only 6-year olds and 8+-year olds explained the variations in natural mortality [$\alpha_{a,j}$ parameter $\neq 0$ in Equation (3)]; this effect was only significant for 1-year olds for which 6-year olds had a negative density-dependent effect ($t = -3.77$, $p = 0.005$) and 8+-year olds a positive one ($t = 5.05$, $p < 0.001$). When non-significant density-dependence was removed from Equation (3), previously significant terms were no longer significant. Density-dependent effects on natural mortality were therefore not included in the final model. In that case, estimates of natural mortality in the absence of cod predation, m_a , were similar between ages, whereas the slopes indicated increasing predation with younger age (Table 2). For example, at average cod SSB for the period 1974–2007, natural mortality was 0.33 and 0.23 for age classes 1 and 8+, respectively.

The number of recruits in the following year exhibited density-dependence with herring SSB of the focal year [Table 3, Equation (5)]. On average for the studied period, the density-dependent effects reduced the per-SSB unit production of recruits by 31% in the Baltic Sea main basin (Table 2).

The effects of year and weight, but not age, on herring growth were significant [Table 3, Equation (7)]. Annual body growth decreased with body weight, so having a stabilizing effect on the population, because productivity depends on BM. The year-growth parameter k_y was a random parameter (hence the mixed model), and it decline markedly from 1987 to 1990. Together with cod SSB, it was the most prominent indicator of environmental change in the period (Figure 1).

When estimating the weight of recruits, the intercept m of Equation (8) was not significant, so Equation (8) was refitted without an intercept (Table 3). The average weight-at-age of the recruits was 37% of the average parental weight (Table 2). The year effect in the analyses of BM growth above was tested, but found to be not significant (Table 3).

Environmental conditions

Fourier analysis was carried out on cod SSB and the year-growth factor [Equation (7)] to obtain explanatory variables for contrasting environmental conditions based on the highest spectral densities of the two series that represented long-term changes. For cod

SSB, the periods of the four highest spectral densities were 34, 17, 11.3, and 8.5 years, whereas for year growth, the three highest spectral densities had periods of 34, 17, and 11.3 years. The fitted Fourier function for cod SSB from 1974 to 2007 had a maximum of 680 000 t, which is representative for the period 1980–1984, and a minimum during 1998–2007, during which it averaged $\sim 100\,000$ t (Figure 1). These maximum and minimum values are considered to be representative of cod SSB. The maximum rate of change of the Fourier function was 85 000 t per year. For year growth, the maximum value was at 0.0095 during 1978–1982, and the minimum value (-0.0004) was around 1995/1996. The value in 2007 (0.0; set as a reference value in the GLM) was very close to this minimum (0.2 s.d.). The maximum rate of change, 0.001 per year, was between 1985 and 1988. We used the values obtained from the Fourier analysis to investigate maximum and minimum conditions in the analysis of F_{MSY} , and also in the scenarios. The minimum values were used to represent the current situation in the Baltic Sea main basin. In the scenarios, the rate of change of the environmental variables was set to the maximum rate obtained from the Fourier analysis.

We then examined which environmental variables among salinity and sprat total biomass best explained the variations in year growth. The year-growth factor exhibited the best correlations with salinity at a depth of 20 m ($r = 0.82$), at station BY29 ($r = 0.70$), and from the first quarter ($r = 0.81$; averaged values for other dimensions, see the “Methods” section). In a GLM for year growth with the three salinity variables, total sprat biomass, total herring biomass, and numbers of herring as explanatory variables, only total sprat biomass ($F_{1,29} = 7.3$, $p = 0.011$) and salinity at 20 m ($F_{1,29} = 8.8$, $p = 0.006$; averaged over station and year) were significant. In a second GLM with an additional categorical dummy variable representing the breakpoint in sprat biomass, year growth increased with salinity (covariate, $F_{1,28} = 38.9$, $p < 0.001$) and decreased with total sprat biomass (covariate, $F_{1,28} = 10.5$, $p = 0.003$), but the analysis revealed a shift in basal growth in terms of the breakpoint ($F_{2,28} = 14.9$, $p < 0.001$). The shift in growth accounted for 12% of the long-term changes in year growth (maximum–minimum). Whatever factor caused this shift in growth, it did not interact significantly with salinity (interaction breakpoint \times salinity, $F_{1,28} = 0.3$, $p = 0.60$) or with total sprat biomass (interaction breakpoint \times spratTBM, $F_{1,28} = 0.2$, $p = 0.65$). The effect of salinity was stronger (a model including the breakpoint and salinity explained just 68% of the variation) than that of sprat total biomass (a model with breakpoint and sprat explained just 43% of the variation).

MSY and target F

For 2007, the MSY for herring was estimated to be 226 000 t, corresponding to $F_{MSY} = 0.16$ (Figure 2). If Baltic cod SSB recovered to 680 000 t without any other changes, the MSY for herring would drop to less than half: 111 000 t at target F_{MSY} of 0.10. In the case that year-growth conditions recovered from today's situation to the historical maximum, the productivity was predicted to more than double, with an MSY value of 482 000 t and $F_{MSY} = 0.27$. With a simultaneous increase in cod SSB, the MSY would be more modest, 315 00 t fished at $F_{MSY} = 0.20$. This situation is close to the conditions in the late 1970s and early 1980s. The recommended target F_{MSY} can then be calculated using

Table 1. Results of the GLM on natural mortality on all age classes of herring.

Effect	SS	d.f.	MS	F	p-value
Age	0.4503	8	0.05629	207.60	0.000
Age \times Age 1	0.0023	8	0.00029	1.06	0.395
Age \times Age 2	0.0022	8	0.00028	1.03	0.413
Age \times Age 3	0.0011	8	0.00013	0.49	0.863
Age \times Age 4	0.0013	8	0.00016	0.59	0.786
Age \times Age 5	0.0033	8	0.00041	1.52	0.152
Age \times Age 6	0.0052	8	0.00066	2.42	0.016
Age \times Age 7	0.0023	8	0.00028	1.04	0.404
Age \times Age 8	0.0071	8	0.00089	3.28	0.002
Age \times Cod SSB	0.0640	8	0.00800	29.50	0.000
Error	0.0521	192	0.00027		

Table 2. Parameters of the operating population model used for central Baltic Sea herring simulations, where the mean square error of the GLM is the sums of squares of the residuals divided by the degrees of freedom of the error.

Model (equation)	Parameter	Description (unit)	Value	t	d.f.	p-value
Mortality (3)	M_1	Natural mortality 1-year olds	0.22985	44.93	1	< 0.001
	M_2	Natural mortality 2-year olds	0.22773	44.52	1	< 0.001
	M_3	Natural mortality 3-year olds	0.22915	44.79	1	< 0.001
	M_4	Natural mortality 4-year olds	0.22735	44.44	1	< 0.001
	M_5	Natural mortality 5-year olds	0.22362	43.71	1	< 0.001
	M_6	Natural mortality 6-year olds	0.22261	43.52	1	< 0.001
	M_7	Natural mortality 7-year olds	0.22258	43.51	1	< 0.001
	M_8	Natural mortality 8-year olds and older	0.22123	43.25	1	< 0.001
	w_{aj}	Density-dependent mortality for all a and j	0			
	V_1	Cod predation on 1-year olds	0.00035	23.76	1	< 0.001
	V_2	Cod predation on 2-year olds	0.00018	12.52	1	< 0.001
	V_3	Cod predation on 3-year olds	0.00012	8.44	1	< 0.001
	V_4	Cod predation on 4-year olds	0.00010	7.04	1	< 0.001
	V_5	Cod predation on 5-year olds	0.00009	6.44	1	< 0.001
	V_6	Cod predation on 6-year olds	0.00008	5.43	1	< 0.001
	V_7	Cod predation on 7-year olds	0.00006	4.14	1	< 0.001
	V_8	Cod predation on 8-year olds and older	0.00005	3.24	1	0.001
	ε	Mean square error of GLM fit of Equation (6)	0.00030			
Reproduction (5)	b	Density-independent reproduction; no. recruits year + 1 (t^{-1})	3.09864	10.24	1	< 0.001
	d	Density-dependent reproduction; no. recruits year + 1 (t^{-2})	-1.05E-06	-3.58	1	0.001
	ε	Mean square error of GLM (t^{-1})	0.55602			
Growth (7)	c	Independent body growth (kg year^{-1})	0.00834	6.88	1	< 0.001
	k_y	Year-specific growth on all ages; listed in Table A2 (kg year^{-1})	0			
	k_a	Age-specific growth (kg year^{-1})	0			
	l	Weight-dependent growth parameter (year^{-1})	-0.13703	-10.23	1	< 0.001
	ε	Mean square error of GLM (kg year^{-1})	0.00007			
Weight of recruits (8)	m	Weight of recruits; intercept (kg)	0			
	k	Parental-weight effect on recruit weight	0.36917	26.03	1	< 0.001
	ε	Mean square error of GLM	0.00002			

Table 3. Results of GLM fitting to herring model functions: recruitment [Equation (5)], growth [Equation (7)], and weight of recruits [Equation (8)].

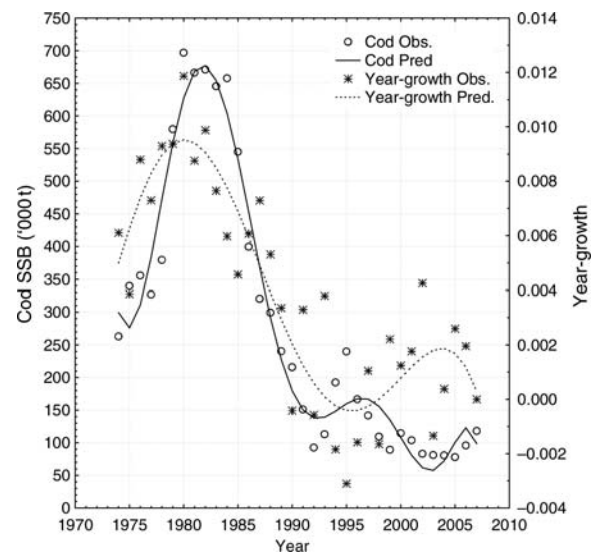
Effect	SS	d.f.	MS	F	p-value
Recruitment function					
Intercept	58.3	1	58.3	104.86	0.000
SSB	7.1	1	7.1	12.81	0.001
Error	17.2	31	0.6		
Growth function					
Intercept	0.000934	1	0.000934	106.70	0.000
Year (R)	0.001717	33	0.000052	6.65	0.000
Age	0.000070	5	0.000014	1.78	0.119
Weight	0.000284	1	0.000284	36.32	0.000
Error	0.001282	164	0.000008		
Weight of recruits function					
Intercept	0.000016	1	0.000016	1.04	0.315
Average parent weight	0.000165	1	0.000165	10.61	0.003
Year growth	0.000003	1	0.000003	0.22	0.640
Error	0.000467	30	0.000016		

linear interpolation over year growth G and cod SSB C :

$$F_{\text{MSY}} = 0.175 + 11.3 G - 0.000104 C - 0.00174 GC, \quad (10)$$

and similarly, the yield achieved

$$\text{MSY} = 256 + 26800 G - 0.202 C - 9.06 GC. \quad (11)$$

**Figure 1.** Plot of environmental variables. Cod SSB estimates (open circles; ICES, 2009a) and the estimated year-growth factor (stars) from the growth model [Equation (7)]. Lines represent fitted Fourier models for cod SSB (continuous line) and year growth (broken line).

The range of F values in which the mean yield is kept within 95% of the maximum is a measure of how sensitive the expected yield is to variations in fishing mortality (i.e. how accentuated is the

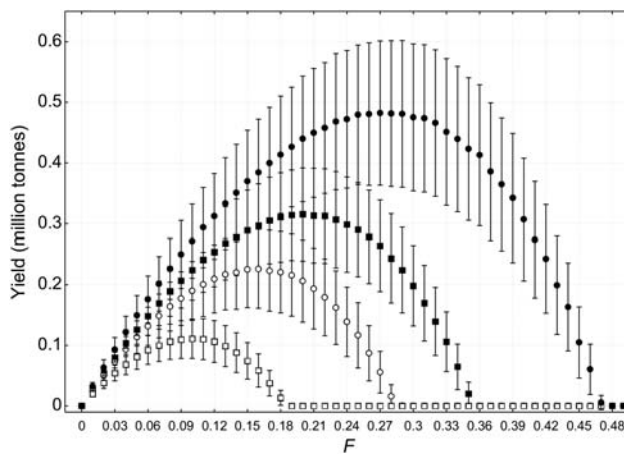


Figure 2. Expected yield in relation to fishing mortality F . Filled symbols represent high, and open symbols low, year growth; squares are high and dots low cod SSB. Error bars represent the s.d. of the yield.

peak of the yield curve). The 95% mean-yield ranges of the F values are 0.08–0.12, 0.13–0.19, 0.17–0.23, and 0.23–0.32, but the variation in yield between individual years is considerable (Figure 2). This variation is the result of the added random error of the four model functions [Equation (1)] and the random error added to the environmental variables.

Scenario results

Changes in SSB

Assuming the current conditions for cod SSB and food availability (for which year growth is a proxy), herring SSB was predicted to increase to double its size, 1.2 million tonnes, in 25 years (Figure 3a). This applies only if fishing mortality is maintained at $F_{MSY} = 0.16$. In the scenario with a successive cod SSB recovery over 7 years, to the peak levels of the early 1980s, fishing mortality should be adjusted annually, applying Equation (10). When doing so, herring SSB is still predicted to increase for about a decade until it levels off at 800 000–900 000 t (Figure 3a). In the third scenario, with an increase in year growth only and a corresponding adjustment in F_{MSY} , Equation (9), an increase in herring SSB up to 1.4 million tonnes was predicted. The rate of change of the herring SSB tracked the change in year growth, both ceasing after 10 years of increase. When both cod SSB and year growth were forecast to increase, the SSB increased faster than under the unchanged scenario, but the two curves met after 18 years at approximately the same level. However, the results from the scenario simulations showed great variation between runs because of the annual variation in herring population processes [Equations (3), (5), (7), and (8)] and in the environmental variables (Figure 1). The 95% outcome interval overlapped considerably for single years and almost encompassed the averages of all four scenarios (Figure 3a).

Weight-at-age changes

There was an increase in weight-at-age of herring only if year growth increased from the current low situation. In that case, weight-at-age regained the values of the early 1980s (Figure 3b). Without an increase in year growth, weight-at-age would not change much, though avoiding the extreme low values of the late 1990s. Around 1995, there were also some observed year-growth values that were

markedly below the fitted Fourier curve (Figure 1). There was great variation in weight-at-age between simulations, but there was no overlap between 25 percentiles and for the 8+ age class, not even between 2.5 percentiles when comparing low year-growth simulations with high year growth (Figure 4).

Discussion

If MSY-based advice is followed and management is implemented successfully, the stocks about which ICES is concerned are currently in transition from the levels generated by a precautionary approach to levels at which MSY is achieved. The 2011 ICES recommendation for herring in the Baltic Sea main basin was the first based to be on a target $F_{MSY} = 0.19$ (ICES, 2010). Here, we provide a tool for setting a target F_{MSY} [Equation (10)] based on cod SSB and food availability. The proxy for food availability, the statistical estimate of year-specific body growth, was correlated with sprat total biomass and salinity, which have been suggested previously as causal factors for food availability (Casini *et al.*, 2010). The analyses here for the past decade lead to a target F_{MSY} of 0.16, but year-specific targets need to take into account the latest estimate of cod SSB and the calculated year growth. A historical application of the method reveals that fishing mortalities were close to the simulation-generated proposals of F_{MSY} from 1974 to 1988, and the yields were roughly what would be expected as MSY (Figure 5). During the years 1989–2003, the fishing mortality estimated by ICES was clearly greater than the target F_{MSY} . When quotas regulated by F were converted to TAC in weight, the F increased if body weight decreased, so the rapid drop in weight-at-age between 1987 and 1990 was probably the main reason for the increased F in from 1989 to 2003 (ICES, 2010). It was not until a decade later that yields began to diverge noticeably from the predicted yields (=MSY). Therefore, there was no obvious short-term benefit in terms of landings, from a higher exploitation rate, except perhaps for the first year of overexploitation. It seems that today's yields are still relatively low because of the seeming over-exploitation in the 1990s, though fishing mortality has been close to F_{MSY} since 2004. The price of landed herring depends on its size, but given a value of €200 per tonne (<http://fis.com/fis/worldnews/worldnews.asp?monthyear=&day=4&id=35410&l=e&special=0&ndb=0>), the net loss as a consequence of the over-exploitation is estimated to have been €440 million. Expressed as a consumer price, though, it can be 20 times higher, or more, depending on country.

Density-dependence is an essential property of stocks if they are to be harvested at an MSY (Milner-Gulland and Mace, 1998). MSY is achieved by harvesting the annual production (i.e. the productivity) of the population. Productivity is usually defined as the annual increase in biomass of the population, given the impact of ecosystem effects other than fishing. Therefore, productivity includes net population growth in numbers, BM growth of individuals, and the effects of predation, for instance by cod. The productivity increases with population size until a certain biomass, but is reduced non-linearly, giving a maximum level of productivity.

Both the increasing and decreasing terms of the equation influence the maximum level, and both are likely to change as the ecosystem changes. First, the relationship between productivity and stock abundance may vary over time. In herring and many other species, fecundity depends on the BM of reproductive individuals, because large individuals produce more roe (Óskarsson and

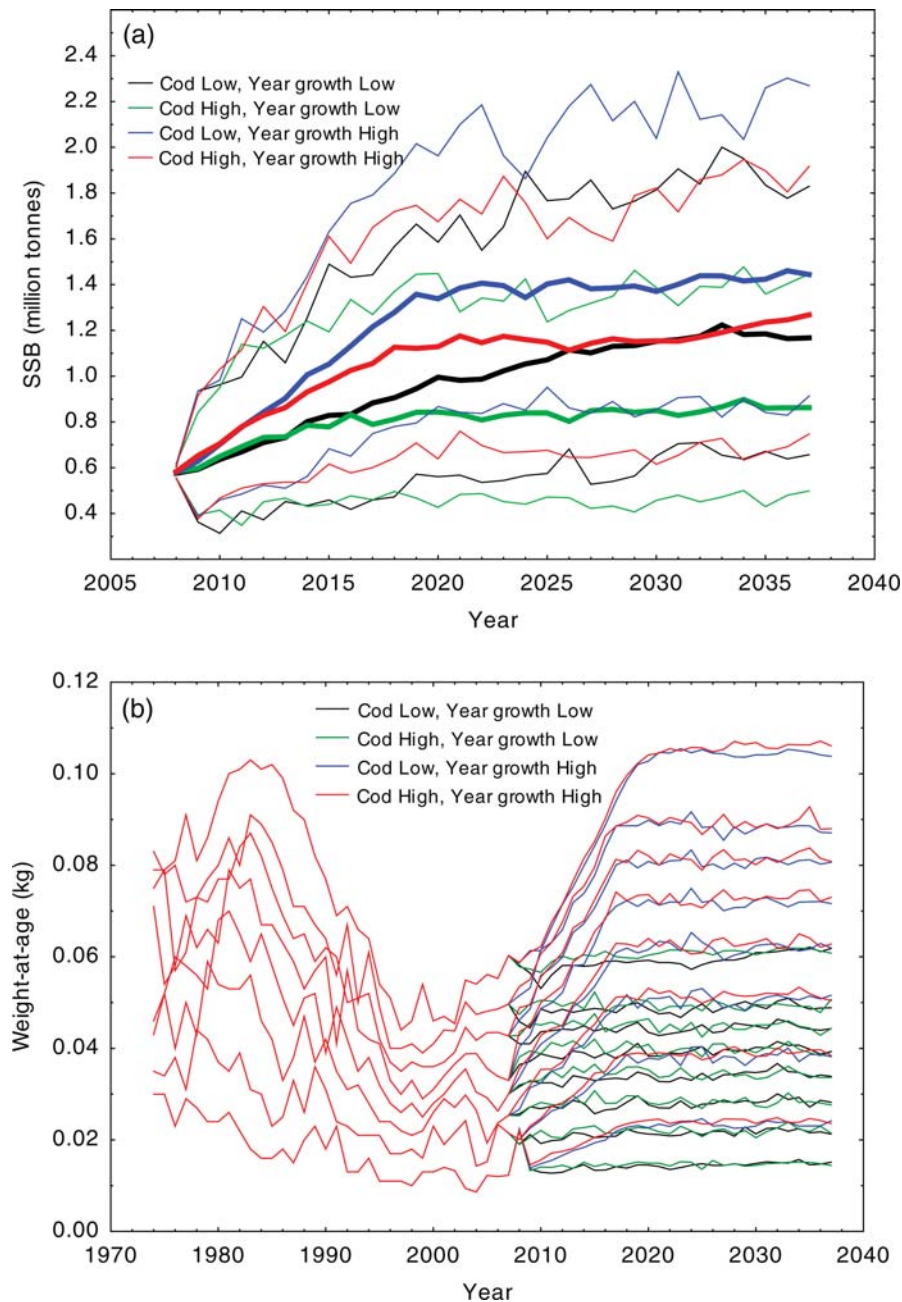


Figure 3. Forecasts for 30 years from 2008 for four scenarios: (a) SSB, (b) weight-at-age (historical values from 1974 to 2007). In (a), the heavy lines denote the averages of 100 MC simulations, and the thin lines 95% outcome intervals of the simulations.

Taggart, 2006). Changes in food availability and body growth, explaining the changes in weight-at-age observed here for Baltic Sea herring, have, according to the analysis, the greatest effect on stock productivity. It appears that during the past 35 years, herring productivity in the Baltic Sea main basin was more influenced by reduced body growth of herring than by predation by cod (Figure 2). Size and condition may be related, but for herring, it seems that body weight (or length) explains more of the potential fecundity than does body condition (Óskarsson and Taggart, 2006), whereas hatching success depends on both female weight and condition (Laine and Rajasilta, 1999). The growth of many fish (following the von Bertalanffy equations) seems to result

from energy reallocation of resources to reproductive investment from an otherwise linear body growth (Lester *et al.*, 2004). After the suggested regime shift in the Baltic Sea, when both herring weight and condition dropped (Flinkman *et al.*, 1998), the total energy available declined, likely affecting the trade-off between reproductive investment and body growth.

The other term of the equation, the negative effect of density-dependence on productivity, may have biotic and abiotic causes, and is unlikely to be constant (Casini *et al.*, 2010), especially when depending on biotic factors. This can make density-dependence hard to detect and with a large standard error in its estimate. It is commonly acknowledged that it is problematic to

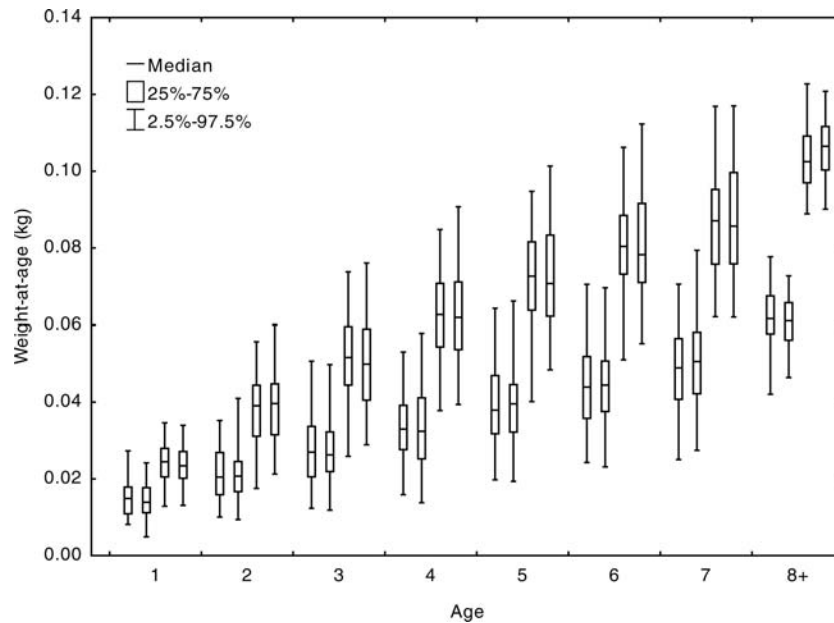


Figure 4. Percentile plot of the weight-at-age outcomes from the scenarios recorded after 30 years of simulations. Boxes are grouped by age class, with the scenarios from left to right for each age class: unchanged, increased cod SSB, increased year growth, and both cod SSB and year-growth increased. The mid-bar denotes the median, the box the 25 percentiles and the error bars the 95% outcome interval.

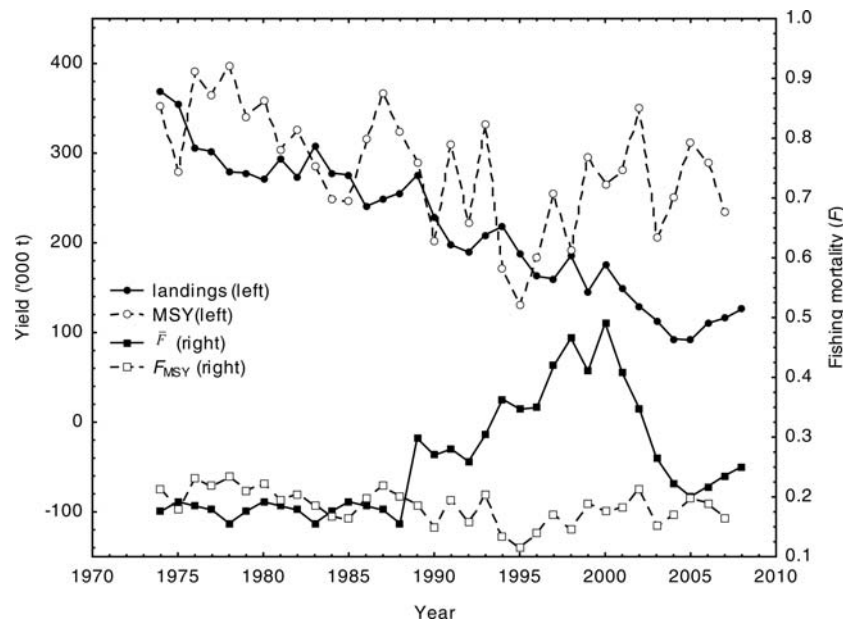


Figure 5. Yield (circles) in relation to fishing mortality (squares) according to historical records (ICES; filled symbols) and if F_{MSY} had been applied about cod SSB and food availability [Equation (10); open symbols]. Cod SSB and the food availability proxy: year-growth values are given as point estimates, as in Figure 1. MSYs are provided by Equation (11).

fit recruitment functions with density-dependence (Walters and Martell, 2004), so we fitted a linearized quadratic function, which has greater sensitivity in detecting density-dependence than non-linear functions with more parameters. Density-dependence in recruits per unit of SSB was clear; however, this was the only density-dependent effect found in the analysis. The mechanism behind this density-dependence may be the food-switching of the main predators of herring larvae

and recruits (Walters and Martell, 2004). Gadoids switch opportunistically to feed on herring eggs during the herring spawning season (Høines et al., 1995), and there is also egg cannibalism among herring to consider (Skaret et al., 2002). If roe-depositing substratum is limited, this would also be a mechanism for density-dependence (Kääriä et al., 1997).

With such a clear effect of weight-at-age on Baltic Sea herring stock productivity, it is important to understand the underlying

mechanisms of food availability, namely salinity-mediated food shortage (Möllmann and Köster, 2002; this study), competition with sprat (Casini *et al.*, 2006; this study), or both, depending on sprat population size. Competition with sprat is the dominant factor when sprat population size is above a threshold level, whereas salinity is the dominant covariant below the threshold (Casini *et al.*, 2010). Looking at the body growth of the cohorts under and over the threshold, the base level (intercepts) of growth was different, but in contrast to previous studies, the dependence (regression slope parameter) on salinity and sprat abundance was the same.

Casini *et al.* (2010) stress that their result could be indicative of hysteresis in ecosystem dynamics and hence of a regime shift (Scheffer and Carpenter, 2003). The results here do lend some support to this notion, but understanding of the mechanisms regulating body growth in Baltic Sea herring is limited. Although food competition with sprat is well documented, it is strange that studies on body growth have failed to detect any significant effect of intraspecific competition (Rönkkönen *et al.*, 2004; Casini *et al.*, 2006; this study). The ability of copepod eggs to hatch after passing through the digestive system of Baltic Sea herring (among other fish; Flinkman *et al.*, 1994), which can be up to 60%, can explain the limited intraspecific competition, but it does not explain the competition with sprat.

From a management perspective, the effect of controlling sprat numbers is still unclear until the competition between clupeid predators and the interaction with the life history of their common prey is better understood. The analyses here suggest that salinity has a notable effect on productivity, explaining 68% of the variation in body growth and indirect variation in fecundity attributable to body size. The overall salinity concentration in the Baltic Sea depends on climate conditions regulating the balance between freshwater run-off and saltwater inflow in winter (Hänninen *et al.*, 2000).

Even if regime shifts and long-term changes in the Baltic Sea are taken into account, interannual variations in the ecosystem and in the population processes still cause considerable variation in the annual yield (Figures 2 and 3). The state of the stock can also deviate considerably from the point when production is maximized, with a loss in productivity and long-term yield. Hence, harvest control rules and catch regulations can potentially be improved to keep stock variations to a minimum, increasing average yields, and reducing interannual variations in landings.

Supplementary material

Supplementary material is available at the *ICESJMS* online version of this manuscript in the form of tables of GLM output explaining the weight of recruits, values of year-specific growth, k_t , from Equation (7), and parameters of non-linear models fitted to the explanatory variables cod SSB and the year-growth factor.

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