International Council for the Exploration of the Sea

C.M. 1993/D:17
Statistics Committee
Ref: J

THE MULTISPECIES STOCK-PRODUCTION MODEL

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ABSTRACT

The multispecies stock - production model is developed, basing on the Andersen and Ursin (1977) analitical model. In the model developed the biomass of a population is dependent on the biomasses of the predator populations, mean weight in the populations, fishing effort or fishing mortality, recruitment and such parameters as von Bertalanffy's growth parameters, food preference parameters, and residual natural mortality. The model is applied to simulate the dynamics of the Baltic cod, herring and sprat stocks. The obtained results are compared with biomass estimates and consumption figures arrived at with other single species and multispecies models. The performed sensitivity analysis shows that the growth parameters have the biggest influence on the model results.

INTRODUCTION

In the past several years, a rapid development of analytical multispecies models had taken place. This occurred in a situation when the intensively developing fishery brought about overfishing of many of the exploited fish stocks, which might result in more intensive interspecific interactions than in a state of an ecological equilibrium. It thus became advisable to take into account the impact of the state of predator stocks on the state of stocks of their prey. Among the most important analytical multispecies models are the following: the Danish model (Andersen and Ursin 1977), which is a complex model of the ecosystem, and the multispecies virtual population analysis (MSVPA) - (Helgason and Gislason 1979, Pope 1979, Sparre 1980). In the Danish model, both the impact of predator abundance on survival rate of their prey and the impact of the state of the food base on the growth rate of fish are considered. The model of the multispecies virtual population analysis is restricted to the study of the impact of the state of predators on the state of prey.

On the other hand, no significant progress has been made in the development of production multispecies models. An example of such a model is the multispecies model of Schaefer (Larkin 1966, Pope 1976, Sullivan 1991). The production models, however - although less precise than the analytical models - are valuable because they do not require as much data as the analytical models. The basis for the use of the production models is catch statistics (catches, fishing effort, CPUE), while it is not necessary to determine the age structure of a population. This makes these models an interesting research tool in the case when it is difficult to determine the age of fish.

The goal of this paper is to propose a new multispecies production model and test it on the populations of cod, herring, and sprat of the Baltic Sea.

THE MODEL

The multispecies stock-production model has been derived on the basis of the analytical multispecies model of Andersen and Ursin (1977). The biomass of age group a of population s in time t may be presented as

$$B_{as}(t) = N_{as}(t)\ w_{as}(t),$$

where N is abundance, and w is weight. Hence

$$dB_{as}/dt = w_{as}dN_{as}/dt + N_{as}dw_{as}/dt.$$

Substituting dN/dt and dw/dt in the above formula with the corresponding formulae from the Andersen and Ursin model (1977) and performing certain algebraic transformations as well as replacing magnitudes and parameters connected with age structure with appropriate approximations or mean values adequate to the population level (see Appendix), we obtain formula

$$\frac{dB_s}{dt} = [v_s h_s/(\bar{w}_s)^{1/3} - F_s - M1_s - k_s - \sum_{r=1}^{n} h_r/(\bar{w}_r)^{1/3}\frac{G_r^s B_r}{\sum_{i=1}^{n} G_r^i B_i}]B_s \qquad [1]$$

where

v, h, k - growth equation parameters from the von Bertalanffy's formula, generalized by Andersen and Ursin (1977),

F - fishing mortality coefficient,

M1 - natural mortality coefficient caused by other reasons than predation,

$\bar{w}$ - mean weight of fish in the population,

G_r^s- suitability of prey s to predator r,

s, r - populations,

n - number of populations.

The above model is a multispecies generalization of the model of Horbowy (1992), in which the author, starting with the main relationships of the single-species Beverton and Holt (1957) model, derived a model which is a differential alternative and an extension of the model of Deriso (1980). The model [1] describes population dynamics between the "moments" of population recruitment. Assuming the term in square brackets being constant or having small variability in a time interval $(t, t + \Delta t)$, model [1] has the following approximate solution

$$B_s(t+\Delta t) = B_s(t)\,\exp[\mathrm{coeff}(t)\Delta t], \qquad [2]$$

where

$$\mathrm{coeff}(t) = v_s h_s/(\overline{w}_s)^{1/3} - F_s - M1_s - k_s - \sum_{r=1}^{n} h_r/(\overline{w}_r)^{1/3} \frac{G_r^s B_r}{\sum_{i=1}^{n} G_r^i B_i} \qquad [2a]$$

In a "moment" of the recruitment to the population, equation [2] will assume the following form

$$B_s(t+\Delta t) = B_s(t)\,\exp[\mathrm{coeff}(t)\Delta t] + R_s, \qquad [3]$$

where R_s is the biomass of the year class recruited to the population.

THE USE OF THE MULTISPECIES STOCK-PRODUCTION MODEL FOR A SIMULATION OF MULTISPECIES INTERACTIONS IN THE BALTIC

Let us try to apply the multispecies model derived for a simulation of multispecies interactions in the Baltic in 1977-1990. In our model cod will be feeding on herring, sprat and "other food" (OT), which covers other small fish and invertebrates. The model will be applied to cod populations from Subdivisions 25-32, herring from Subdivisions 25-29+32, and sprat from the entire Baltic, and restricted to mature fish.

Parameters of the von Bertalanffy's equation for cod were taken from Horbowy (1992). Growth parameters for herring from Subdivisions 25-29+32 and sprat from Subdivisions 22-32 were estimated on the basis of mean individual weights in 1977-1990, in individual age-groups taken from Anon. (1991b).

In order to determine fraction v of the food of cod assimilated for growth, Jobling's studies (1982) were used. Jobling analysed the relationship between the growth of cod from the North Sea and the amount of consumed food; he calculated the following model of efficiency of conversion of food into growth

$$v = 0.688w^{-0.156}$$

where w is individual weight. Using this formula v for the Baltic cod was calculated; it equalled from 0.25 to 0.20 for age range 3-9. For the purpose of this analysis v in the range 0.25-0.20 was assumed, remembering the approximate character of these values.

The level of the coefficient of residual natural mortality was taken from the data of the ICES Working Group on multispecies assessment of Baltic fish (Anon. 1990). The size of initial biomass of cod, herring, and sprat (i.e., biomass in 1977) was taken from Anon. (1991a, b).

The values of the parameters of the model, mentioned above, are presented in Table 1.

Because of the absence of standardized fishing effort for the analysed fish populations, the values of mean arithmetic fishing mortality coefficients, F_{VPA}, estimated by ICES Working Groups on the assessment of fish stocks in the Baltic (Anon. 1991a, b), were used in the simulations as fishing effort indices. Thus, fishing mortality coefficients are being simulated in the model as

$$F = qF_{VPA}$$

where q is the catchability coefficient.

Among the most difficult problems in the application of the model is the determination of the stock - recruitment relationship. Because of the lack of a relationship between the size of spawning stocks and year class abundance for the analysed stocks of Baltic fish, the abundance of year classes, U_{VPA}, estimated by the ICES Working Groups (Anon. 1991a, b), was assumed as their strength index. Hence in our model recruitment abundance is determined according to formula

$$U = \gamma U_{VPA}$$

where γ is an unknown parameter, and the biomass of recruitment is calculated as

$$R = \gamma U_{VPA} o$$

where o denotes the mean weight of fish recruited to the population.

The mean weight values in populations, $\overline{w}$, were calculated by dividing the stocks biomass determined by ICES Working Groups by their abundance.

There remain to be calculated parameters of food preference G, catchability coefficient q, coefficient γ connected with population recruitment, and the "other food" OT. The values of the looked-for parameters G, q, γ, and OT may be estimated by choosing them in such a way as to minimize deviations of the modelled cod, herring, and sprat catches, from the observed catches. When determining these parameters we should take advantage of all existing information about the exploited stocks. In our case, such additional information is cod food composition. We may determine in the model the ratio of sprat biomass consumed by cod to the herring biomass consumed, and then include the deviations of this ratio from the observed ratio in the minimized function of deviations of model magnitudes from the observed ones. The observed mean ratio of the consumed sprat biomass and the consumed herring biomass for 1977–1987, $\hat{BK}_s/\hat{BK}_h$, was taken from the results of the Working Group on multispecies assessment of Baltic fish (Anon. 1990). Finally, we find parameters G, q,

γ, and OT through minimizing the function

$$SS(G_c^s, G_c^h, q_c, q_h, q_s, \gamma_c, \gamma_h, \gamma_s, OT) =$$

$$= \sum_{t=1977}^{1990} \left[\left(\frac{Y_{c,t} - \hat{Y}_{c,t}}{\hat{Y}_{c,t}} \right)^2 + \left(\frac{Y_{h,t} - \hat{Y}_{h,t}}{\hat{Y}_{h,t}} \right)^2 + \left(\frac{Y_{s,t} - \hat{Y}_{s,t}}{\hat{Y}_{s,t}} \right)^2 + \left(\frac{(BK_s / BK_h)_t - \hat{BK}_s / \hat{BK}_h}{\hat{BK}_s / \hat{BK}_h} \right)^2 \right] \qquad [4]$$

where Y denotes model catches, $\hat{Y}$ - observed catches, and indices c, h, and s refer to cod, herring, and sprat, respectively. The minimization was performed using a modified version of the Levenberg-Marquardt algorithm (Brown and Dennis 1972). Parameters G are determined with an accuracy to a constant multiplier, so assuming e.g. $G_c^s=1$, we have only to determine G_c^h. The calculations were made for two assumed values of parameter v: for v = 0.25 and v = 0.20.

The parameters G, q, γ, and OT, estimated for both values of v, and the approximated values of their standard errors are presented in Table 2. The determined parameters differ slightly. The only greater difference occurs in parameters OT - 6000 and 8000 thous. tons for v = 0.25 and v = 0.20, respectively. It should be noted that with the given parameter v, the minimization of the sum of squares [4] has relatively small sensitivity to the choice of the size of "other food" OT (Fig. 1). Only the deviation of the modelled sprat catches from the observed catches exhibits a very distinct minimum.

The majority of the estimated parameters is not correlated with each other (Table 3). Highly correlated are only parameters q_c and γ_c, and γ_h and γ_s (R equalling 0.83 and 0.87, respectively). The explanation of the correlation between γ_h and γ_s is relatively simple. The increasing pressure of cod has a negative impact on the survival rate of both herring and sprat. Hence, in order to achieve in the model the catches similar to those observed, both coefficients γ increase simultaneously, to increase the abundance of recruitment. It is more difficult to explain the positive correlation between q_c and γ_c. One would rather expect a negative correlation here, because of the negative correlation between abundance and fishing mortality at the constant catches.

Table 4 presents biomass values and coefficients of natural mortality due to predation for cod, herring, and sprat, estimated with the help of the model, together with the relative error of the calculated catches of these stocks and the relative error of the modelled quotient of the consumed sprat biomass to the consumed herring biomass, at the assumed value v= 0.25. For v = 0.20, the above magnitudes are very similar. A comparison of the biomass values attained according to the model with the estimates of ICES working groups (Anon. 1991a, b) is shown in Fig. 2. Table 5 presents the size of herring and sprat biomass consumed by cod and, for comparison, the same magnitudes estimated by the Working Group on multispecies assessment of Baltic fish (Anon. 1990) and Horbowy (1989). When comparing these estimates it should be borne in mind that the present model uses populations of mature fish (age 3+ for cod, 2+ for herring and sprat), while the other estimates cover also age-groups 0 and 1. Taking the above into account it may be said that the presented estimates of the biomass consumed by cod are similar. When attempting to compare the obtained coefficient of natural mortality due to predation with estimates from other sources, it should be remembered that in the model presented M2 may be interpreted as an arithmetic mean of natural mortality coefficients in age-groups, weighted by the biomass of these age-groups.

SENSITIVITY ANALYSIS

The sensitivity analysis of the model was based on an ordinary sensitivity analysis and extended stochastic sensitivity analysis (Majkowski et al. 1981). In the ordinary sensitivity analysis, the reaction of the modelled biomasses to changes in the values of the assumed parameters of the model (Table 1) and the parameters determined through the minimization of function [4] (Table 2) by 1, 5, 10, 20, and 50% were studied. In the extended stochastic analysis it was assumed that the parameters of the model have approximately normal distribution. Knowing standard deviations of these parameters (Tables 1 and 2), their distributions may be determined. Standard deviations of the parameters taken from the literature, i.e., v, B0, M1, were not known; it was arbitrarily assumed that the standard deviation of v equals 20%, that of B0 - 20%, and that of M1 - 25% of the parameter value. Sensitivity analyses were performed next, calculating deviations of biomasses of cod, herring, and sprat at disturbed parameters from biomasses at undisturbed parameters after simulating 1, 5, and 10 years of stocks interactions. The starting year for the simulation was 1977. In the ordinary sensitivity analysis, biomass deviations were presented in percent, and in the extended stochastic sensitivity analysis - as a ratio of the biomass at disturbed parameters to the biomass at undisturbed parameters. In the extended stochastic sensitivity analysis, the simulation with the model was repeated 500 times.

The ordinary sensitivity analysis of the model reveals that the greatest influence on errors of the model has the accuracy of growth parameters; v, h, k. The disturbance in the values of these parameters results in a change of the biomass of their corresponding population at a level usually smaller than the level of disturbance after 1st simulated year. After the 5th simulated year the change in biomass is most often higher than the value of disturbance of v or h, and after the 10th simulated year the change in biomass may be even several times higher than the level of disturbance of these two growth parameters. The model is less sensitive to errors in parameter k; when the disturbance overestimates the value of the parameter, the change in the modelled biomass is usually lower than the value of the disturbance, while at the underestimated value of k, the change in the biomass may be very high. The errors in parameters v, h, and k for cod influence also the errors of the modelled biomasses of herring and sprat, these errors usually not being higher than the errors of the parameters. Disturbances in the remaining parameters of the model cause changes in the calculated biomasses at a level usually not exceeding the disturbance of the parameter even after the 10th simulated year.

The results of the extended sensitivity analysis of the model are presented in Table 6. All distributions of the ratio of the disturbed biomass to undisturbed biomass are skew, the skewness of the distributions increasing with the time of simuulations. The skewness of the distributions results from the model [2] being exponential and the assumed normal distributions of errors of the model parameters. Geometric means of the obtained ratios of the disturbed biomasses to the undisturbed biomasses are close to one. Standard deviations for cod and herring are small, especially after 1st and 5th simulated year. Standard deviation of the error distribution for sprat after the tenth simulated year is very high. One may say with some approximation that 50% of the observed ratios of the disturbed biomasses to the undisturbed biomasses lie in the 0.5-1.5 interval but there are also - mainly for sprat - extremely high values. The disturbed biomass may be, as a result of especially unfavorable cumulation of parameter errors, several thousand times higher than the undisturbed biomass after the tenth simulated year, although the probability of such an occurrence is smaller than 1%. This points to the necessity of exercising caution when making a prognosis of the dynamics of the population in a period of about 10 years. We are ignoring here the question, whether it is rational to make a biomass prognosis for such a long time, especially for population dynamics of Baltic fish, extremely dependent on environmental conditions. A prognosis for a period of 1-5 years is possible from the point of view of the model sensitivity, although considerable errors of the modelled biomass for sprat may also appear here.

ACKNOWLEDGEMENTS

I would like to thank the State Committee for Scientific Research (KBN) for providing funds for this research (grant No. 5 5480 91 02).

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APPENDIX

We will present the derivation of model [1]. Let us begin with a reminder of the basic relationships of the Andersen and Ursin model (1977), which is the starting point for further considerations. In the Andersen and Ursin model changes in abundance, N, mean weight, w, and cumulated catch, Y, are described by the following set of differential equations

$$dN_{as}/dt = -(F_{as} + M1_{as} + M2_{as})\, N_{as} \qquad [1a]$$

$$dw_{as}/dt = v_s h_s f_{as} w_{as}^{2/3} - k_s w_{as} \qquad [1b]$$

$$dY_{as}/dt = F_{as} N_{as} w_{as} \qquad [1c]$$

where: t - time, F - fishing mortality coefficient, M2 - coefficient of natural mortality due to predation, M1 - coefficient of natural mortality due to other reasons than predation, f - indicator of the size of consumed food ration, v, h, k - parameters of growth equation, a - age-group, s - species (population). The values of M2 and f are modelled with equations

$$f_{as} = P_{as}/(P_{as} + Q_{as}) \qquad [2]$$

$$M2_{as} = \sum_{r=1}^{n} \sum_{b=1}^{m_r} h_r G_{br}^{as} N_{br} w_{br}^{2/3} f_{br}/P_{br} \qquad [3]$$

$$P_{as} = \sum_{r=1}^{n} \sum_{b=1}^{m_r} G_{as}^{br} N_{br} w_{br}, \qquad [4]$$

where: P - available food, Q - parameter defining food demands of the population, G_{br}^{as} - indicator of preference as food of age-group a of population s by age-group b of population r, n - number of populations considered, m_r - number of age-groups in population r.

Let us proceed now to the derivation of the multispecies stock - production model. Let B_{as} denote biomass of age-group a of population s. Then

$$B_{as} = N_{as} w_{as}.$$

Differentiating the above equation we obtain

$$dB_{as}/dt = (dN_{as}/dt)\, w_{as} + N_{as}(dw_{as}/dt) \qquad [5]$$

Next, we will assume the constant magnitude of feeding level f; we will also assume that f = 1. Thus, formula [3] will assume the form

$$M2_{as} = \sum_{r=1}^{n} \sum_{b=1}^{m_r} h_r G_{br}^{as} N_{br} w_{br}^{2/3}/P_{br} \qquad [6]$$

Substituting in equation [5] formulae [1a, b] and [6] and ignoring f we have

$$dB_{as}/dt = -(F_{as} + M1_{as} + \sum_{r=1}^{n} \sum_{b=1}^{m_r} h_r G_{br}^{as} N_{br} w_{br}^{2/3}/P_{br}) N_{as} w_{as} +$$

$$+ (v_s h_s w_{as}^{2/3} - k_s w_{as}) N_{as} = v_s h_s N_{as} w_{as}^{2/3} -$$

$$- (F_{as} + M1_{as} + k_s + \sum_{r=1}^{n} \sum_{b=1}^{m_r} h_r G_{br}^{as} N_{br} w_{br}^{2/3}/P_{br}) B_{as}.$$

Adding the above equations according to age-groups within the population and replacing magnitudes G_{br}^{as} and P_{br} with adequate averaged values for the populations, G_r^s and P_r and assuming that F and M1 are not age dependent, we obtain

$$dB_s/dt = \sum_{a=1}^{m_s} dB_{as}/dt = v_s h_s \sum_{a=1}^{m_s} N_{as} w_{as}^{2/3} -$$

$$- \sum_{a=1}^{m_s} (F_s + M1_s + k_s + \sum_{r=1}^{n} \sum_{b=1}^{m_r} h_r N_{br} w_{br}^{2/3} G_r^s/P_r) B_{as} =$$

$$= v_s h_s \sum_{a=1}^{m_s} N_{as} w_{as}^{2/3} - (F_s + M1_s + k_s + \sum_{r=1}^{n} h_r G_r^s/P_r \sum_{b=1}^{m_r} N_{br} w_{br}^{2/3}) \sum_{a=1}^{m_s} B_{as}.$$

Thus we have

$$dB_s/dt = v_s h_s \sum_{a=1}^{m_s} N_{as} w_{as}^{2/3} - (F_s + M1_s + k_s + \sum_{r=1}^{n} h_r G_r^s/P_r \sum_{b=1}^{m_r} N_{br} w_{br}^{2/3}) B_s \qquad [7]$$

In further transformations we will use the following identity

$$\sum_{a=1}^{m_s} N_{as} w_{as}^{2/3} \Big/ \sum_{a=1}^{m_s} N_{as} w_{as} = \overline{w}_s^{2/3}/\overline{w}_s,$$

resulting from the definitions of the means $\overline{w}^{2/3}$ and $\overline{w}$ (Horbowy 1992). Thus

$$\sum_{a=1}^{m_s} N_{as} w_{as}^{2/3} = (\overline{w}_s^{2/3}/\overline{w}_s) B_s$$

and substituting the above formula in equation [ ] we arrive at

$$dB_s/dt = v_s h_s (\overline{w}_s^{2/3}/\overline{w}_s) B_s - [F_s + M1_s + k_s + \sum_{r=1}^{n} h_r G_r^s/P_r (\overline{w}_r^{2/3}/\overline{w}_r) B_r] B_s$$

Presenting mean available food resources for the population as

$$P_r = \sum_{i=1}^{n} G_r^i B_i ,$$

we will finally obtain

$$dB_s/dt = [v_s h_s(\overline{w_s^{2/3}}/\overline{w}_s)-F_s-M1_s-k_s-\sum_{r=1}^{n} h_r(\overline{w_r^{2/3}}/\overline{w}_r)\frac{G_r^s B_r}{\sum_{i=1}^{n} G_r^i B_i}]B_s \qquad [8]$$

Let us add that in practice the ratio $\overline{w^{2/3}}/\overline{w}$ may be replaced by the magnitude $(\overline{w})^{-1/3}$. Although generally $\overline{w^{2/3}}/\overline{w}$ differs from $(\overline{w})^{-1/3}$ both these magnitudes are highly correlated and a regression coefficient is close to one (Horbowy 1992). Substituting $\overline{w^{2/3}}/\overline{w}$ with magnitude $(\overline{w})^{-1/3}$ we express the model in a more elegant form

$$dB_s/dt = [v_s h_s/(\overline{w}_s)^{1/3}-F_s-M1_s-k_s-\sum_{r=1}^{n} h_r /(\overline{w}_r)^{1/3}\frac{G_r^s B_r}{\sum_{i=1}^{n} G_r^i B_i}]B_s \qquad [9]$$

The using of the model for catch projection will require mean weight in the stock being a function of the exploatation intensity. It may be easily shown that mean weight at the begining of the year y+1 can be approximated as

$$w_{y+1}= \frac{R_{y+1} + B_y \exp[coeff(y)]}{U_{y+1} + B_y \exp(-Z_y)/w_y}$$

where coeff(y) is the term in square brackets in model [9] and Z is the total mortality coefficient.

TABLES

Table 1. Values of parameters of the differential form of the von Bertalanffy's growth equation, H and k, together with their standard errors, sd, coefficient of residual natural mortality, M1, mean weight (in g) of fish recruited to the population, o, and initial biomasses, BO (thous. tons), for cod, herring, and sprat.

Stock	Cod	Herring	Sprat
H	0.968	2.84	5.13
sd	0.097	0.26	0.47
k	0.46	0.57	2.00
sd	0.05	0.067	0.20
M1	0.2	0.2	0.2
o	437	26.5	10.0
BO	421	2057	1161

Table 2. Determined parameters G, q, and γ for cod, herring, and sprat, size of other food OT, standard deviation of parameters, sd, and the square root of minimum of function [4], se, for v = 0.25 and v = 0.20 (c - cod, h - herring, s - sprat).

Parameter	v=0.25	sd	v=0.20	sd
G_c^s	1.000	-	1.000	-
G_c^h	0.561	0.088	0.556	0.088
q_c	0.604	0.048	0.605	0.048
q_h	0.875	0.122	0.875	0.122
q_s	0.377	0.056	0.380	0.056
γ_c	0.666	0.094	0.668	0.093
γ_h	1.038	0.116	1.033	0.116
γ_s	1.246	0.214	1.234	0.214
OT	6000.030	1647.000	8000.023	2085.300
se	0.188	-	0.188	-

Table 3. Coefficients of correlation among parameters G, q, γ and OT for cod, herring, and sprat, determined through minimalization of the sum of squares [4] (c - cod, h - herring, s - sprat).

Parameter	q_c	q_h	q_s	γ_c	γ_h	γ_s	OT
G_h	-0.02	0.38	-0.56	0.00	0.09	0.26	0.19
q_c		0.05	0.08	0.83	-0.28	-0.28	0.12
q_h			0.32	0.00	-0.17	-0.12	-0.20
q_s				0.02	-0.33	-0.44	-0.29
γ_c					-0.14	-0.13	0.16
γ_h						0.87	-0.63
γ_s							-0.63

Table 4. Biomass values (thous. tons) for cod, herring, and sprat calculated with the help of the model, coefficients of natural mortality due to predation of herring and sprat, relative error (%) of the calculated catches of cod, herring, and sprat, and relative error of the calculated ratio of consumed sprat biomass to consumed herring biomass at v = 0.25 (c - cod, h - herring, s - sprat).

Year	Biomass			Predation mortality		Relative error (%) of catch			consumption
	c	h	s	h	s	c	h	s	
1977	424	2057	1161	0.11	0.19	-19	-15	16	7
1978	444	1974	1140	0.12	0.21	2	11	1	7
1979	617	1939	920	0.17	0.31	12	16	0	-15
1980	752	1638	760	0.21	0.37	10	20	-27	-17
1981	740	1443	563	0.21	0.37	-2	20	6	-43
1982	721	1503	704	0.20	0.36	-1	36	-8	-14
1983	738	1553	665	0.21	0.38	8	26	2	-30
1984	752	1548	1252	0.20	0.35	8	7	-20	37
1985	641	1705	1296	0.16	0.28	15	-14	14	32
1986	561	1763	1272	0.14	0.24	-25	-29	15	27
1987	410	1573	1041	0.10	0.19	-2	-6	22	19
1988	360	1924	1187	0.09	0.16	13	-1	13	16
1989	326	1798	1053	0.09	0.15	1	-7	23	7
1990	247	1905	2015	0.05	0.09	10	-19	-1	51

Table 5. Consumed biomass, BK (thous. tons) of herring and sprat calculated according to the model and determined by Horbowy (1989) and after Anon. (1990) (h - herring, s - sprat).

Year	The model BK_h	BK_s	Horbowy (1989) BK_h	BK_s	Anon. (1990) $BK_h + BK_s$
1977	197	196	219	203	475
1978	206	205	228	186	604
1979	280	226	285	217	754
1980	282	223	282	340	709
1981	242	157	241	406	800
1982	253	205	216	543	876
1983	273	195	219	514	1103
1984	250	368	215	358	866
1985	228	310			579
1986	209	265			357
1987	144	165			389
1988	159	175			332
1989	137	136			281
1990	93	175			

Table 6. Results of extended stochastic sensitivity analysis of the model: parameters of distribution of the ratio of biomass at disturbed model parameters to biomass at undisturbed model parameters for cod, herring, and sprat after 1st, 5th, and 10th simulation year.

Parameter	Simulation year 1	5	10
	COD		
Arithmetic mean	1.01	1.10	1.37
Geometric mean	1.00	0.99	0.98
Standard deviation	0.10	0.42	1.21
Minimum	0.75	0.40	0.27
Maximum	1.32	3.17	10.54
Lower quartile	0.94	0.80	0.69
Upper quartile	1.07	1.29	1.57
Standardized skewness	2.7	13.9	32.0
	HERRING		
Arithmetic mean	1.00	1.04	1.09
Geometric mean	0.99	0.98	0.97
Standard deviation	0.10	0.35	0.66
Minimum	0.73	0.41	0.22
Maximum	1.38	3.28	6.80
Lower quartile	0.93	0.81	0.74
Upper quartile	1.06	1.19	1.26
Standardized skewness	4.8	18.1	33.7
	SPRAT		
Arithmetic mean	1.03	1.71	16.77
Geometric mean	1.00	1.16	1.11
Standard deviation	0.26	3.67	48650.0
Minimum	0.45	0.38	0.09
Maximum	2.26	59.52	4586.3
Lower quartile	0.84	0.75	0.49
Upper quartile	1.17	1.51	1.74
Standardized skewness	9.4	105.5	173.0

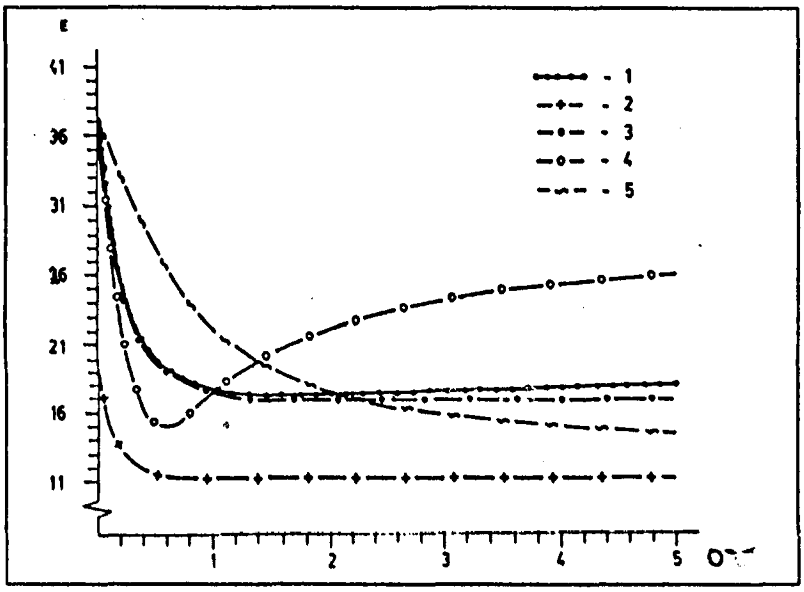

Fig. 1. Dependence of relative error, E (%), of the modelled catches of cod (2), herring (3), sprat (4), of the quotient of consumed sprat biomass to consumed herring biomass (5), and of the total relative error (1) on assumed level of "other food", OT (10^7 tons) at v = 0.25.

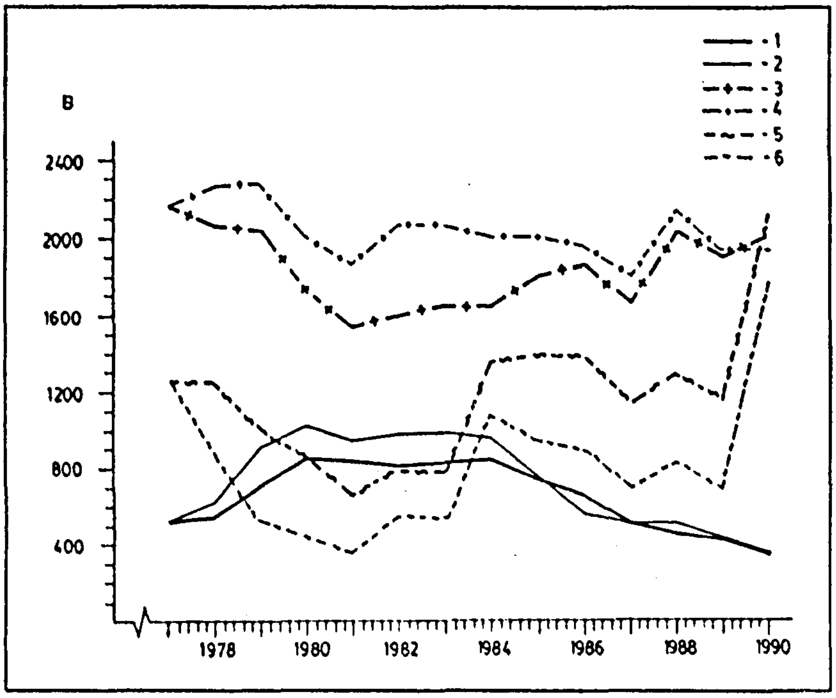

Fig. 2. A comparison of the biomass B (10^3 tons), of cod (1), herring (3), and sprat (5) estimated with the help of the model, with corresponding estimates obtained by virtual population analysis (Anon. 1991a, b)(cod (2), herring (4), sprat (6)).