# A multispecies model of fish stocks in the Baltic Sea

*Jan Horbowy*
Sea Fisheries Institute, Al. Zjednoczenia 1, 81-345 Gdynia, Poland

## Abstract

The Andersen and Ursin multispecies stock assessment model has been slightly modified and used to simulate interactions between cod, herring, sprat, benthos and zooplankton in Sub-divisions 25-29S of the Baltic in the years 1974-1984. The main modifications were: including intraspecific competition into the feeding level formula and introducing a prey biomass-dependent preference index. The model has been verified by comparing simulated yield, age at catch, growth of fish, and cod food composition with appropriate observed values. Finally, a number of fishing strategies where fishing mortality and age at full capture of cod were changed under the simulations.

## Introduction

A relatively simple system of trophic levels in the Baltic Sea makes it easy to apply multispecies models for the evaluation of predator-prey interactions, which may form the basis for more precise stock assessment, catch prediction, and determination of an optimal fishing policy. Several authors (Mandecki, 1976; Majkowski, 1977; Horbowy & Kuptel, 1980) have undertaken such an approach on the basis of the Danish multispecies model (Andersen & Ursin, 1977).

Mandecki (1976) used the Danish multispecies model to simulate the relationships between cod, herring, sprat and zooplankton in the Baltic. He limited himself to modeling the impact of the predator stock on the survival rate of its prey, without taking into account the dependence of individual growth on the amount of food resources. This author found that the observed fluctuations in the catches of Baltic fish may be explained, in part, by the predator–prey interactions between the stocks of cod and herringlike fish. He calculated that, in order to attain a maximum catch or maximum profits, the cod stock should be eliminated entirely so that herring and sprat could be exploited in the total absence of their predator. He then assumed that the sum of fishing mortality coefficients was constant and determined the values leading to maximum catches. It turned out that these values approached the actual and the author, thus, concludes that the Baltic fishery exhibits an exploitation pattern similar to the optimal.

Majkowski (1977) used the Danish model to simulate interactions between cod, herring and sprat in the Baltic proper, taking into account both the impact of the predator stock on the mortality of prey and biomass of prey on the predator growth. Like Mandecki, he found that interactions of the type: predator-prey influenced the fluctuations in Baltic fish catches and predicted their size for a few following years.

Horbowy & Kuptel (1980) did not introduce anything totally novel to multi-species modeling. These authors concentrated on various stocks of cod, herring and sprat in the Baltic Sub-divisions 24-29S, cod feeding migrations and introducing into the model zooplankton and benthos as external variables. Their catch predictions were based on several different stock exploitation patterns.

In 1981 the ICES Working Group on Multispecies Assessment of the Baltic Fish met for the first time to 'discuss multispecies assessment of the Baltic fish and to advise on any data deficiencies' (Anon., 1981) focussing on simulation of an appropriate data base.

In the above mentioned applications based on the Andersen & Ursin (1977) approach, some of the basic model's parameters were determined within the modeled catches with observed ones. Thus, using the model parameters determined independently of it and taking into account some other criteria of its credibility (e.g. a comparison of the modeled and observed food and growth of fish) should increase its value. The present author also introduces certain modifications to the Danish model aimed at a fuller presentation of trophic relationships and population dynamics.

## The Model

The multispecies stock assessment model of Andersen & Ursin (1977) is expressed by the following set of the basic differential equations

$$(dN_i/dt) = -(F_i + M1_i + M2_i)\, N_i$$

$$(dw_i/dt) = v_i h_i f_i w_i^{2/3} - k_i w_i \qquad i = 1, 2, \ldots, n$$

$$(dY_i/dt) = F_i N_i w_i$$

where

$$f_i = \phi_i/(\phi_i + Q_i)$$

$$M2_i = \sum G_{ij} h_j w_j^{2/3} N_j/(\phi_j + Q_j)$$

$$\phi_i = \sum G_{ji} N_j w_j$$

$$Q_i = V/q_i'$$

$$G_{ij} = \rho_{ij} g_{ij}$$

$$g_{ij} = \exp(-(\ln(w_j/w_i) - \eta_j)^2/(2\sigma_i^2))$$

where

$N, w, Y$ – numbers, mean weight and yield, respectively,

$F, M2, M1$ – fishing mortality, natural mortality caused by predation and natural mortality from other sources, respectively,

$f$ – feeding level,

$\phi, Q$ – available food and half saturation constant, respectively,

$V$ – water volume,

$q'$ – search rate coefficient

$r$ – positive parameter determining biomass concentration–weight relationship,
$v$, $h$, $k$ – growth parameters,
$G_{ij}$ – total preference of prey $i$ by predator $j$,
$g_{ij}$ – size preference of prey $i$ by predator $j$,
$\eta$, $\sigma$ – food size preference parameters,
$\rho_{ij}$ – vulnerability of prey $i$ to predation by predator $j$,
$i$, $j$ – entity (age group or life stage),
$n$ – number of entities.

Some modifications of the Danish model were made in order to better reproduce trophic relationships. These are:

### Modification of the feeding level

In the Danish model, feeding level depends on the amount of food available to predators. Here, feeding level was modified so that it was also dependent on predator numbers. It was assumed that the search rate coefficient $q_i{}'$ is inversely proportional to the number of fish, $NS_i$, competing for food $\phi_i$

$$q_i{}' = \alpha / NS_i$$

where $\alpha$ is a parameter. Thus, in the present approach

$$Q_i = q_i NS_i$$

where $q_i = V / \alpha$. Now the feeding level of the entity is being formulated as

$$f_i = \phi_i / (\phi_i + q_i NS_i) = (\phi_i / NS_i)/(\phi_i / (NS_i + q_i))$$

depends on the available food biomass per fish competing for food $\phi_i$. Only intraspecific competition was considered and it was assumed for simplicity that, for the given age only one year older and one year younger age groups of a species compete for food so

$$NS_i = A_{i-1}{}^i N_{i-1} + N_i + A_{i+1}{}^i N_{i+1}$$

and

$$A_k{}^i = G_{jk} (dR_k / dt)_{\max}/(dR_i / dt)_{\max} \quad , k = i-1, \ i+1$$

where $dR / dt$ is consumption rate from the Andersen & Ursin model. Coefficients $A_k{}^i$ express the strength of the competition. They are defined as the preference of the preferred food of entity $i$ (say entity $j$) by the entity $k$, multiplied by the ratio of the maximum consumption of these entities. As $dR/dt = hfw^{2/3}$ and $\rho_{jk} = 1$, we have

$$A_k{}^i = g_{jk}(w_k / w_i)^{2/3}$$

for $k = i - 1, \ i + 1$ (Fig. 1).
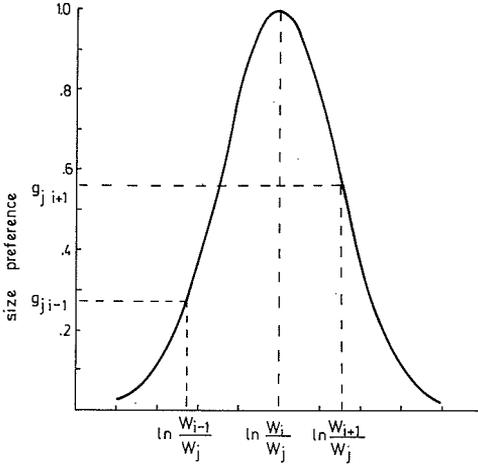
Fig. 1. Geometrical interpretation of the size preference $g_{jk}$ included in the formula for the coefficient $A_k{}^i$. $W_i$ is predator weight, $W_j$ is prey weight.

## Prey biomass-dependent preference index

Ivlev (1955) observed that predators can change their electivity when the biomass of prey changes. Food positively elected can be omitted when its biomass drops markedly while food previously avoided can be positively elected. The analysis of the Baltic cod stomach contents indicates that cod increases its preference for herring when the ratio of herring to sprat biomass increases. Similarly, cod's preference for zooplankton and benthos increases when the biomass of herring-like fish biomass to cod biomass ratio declines. Thus, the cod prey biomass-dependent preference index, $p$, for herring, sprat, zooplankton and benthos has been modeled as

$$p_h = \begin{cases} A1\ \mathrm{Th}(B_h/B_s - A2) + A3 & \text{for } A1\ \mathrm{Th}(B_h/B_s - A2) + A3 \leq 1/\rho_h \\ 1/\rho_h & \text{for } A1\ \mathrm{Th}(B_h/B_s - A2) + A3 > 1/\rho_h \end{cases}$$

$$p_s = \begin{cases} 1 & \text{for } A1\ \mathrm{Th}(B_h/B_s - A2) + A3 \leq 1/\rho_h \\ 1/[\rho_h(A1\ \mathrm{Th}(B_h/B_s - A2) + A3)] & \text{for } A1\ \mathrm{Th}(B_h/B_s - A2) + A3 > 1/\rho_h \end{cases}$$

$$p_b = \begin{cases} a1\ \mathrm{Th}(B_c/(B_h + B_s) - a2) + a3 & \text{for } a1\ \mathrm{Th}(B_c/(B_h + B_s) - a2) + a3 \leq p_b{}^{max} \\ p_b{}^{max} & \text{for } a1\ \mathrm{Th}(B_c/(B_h + B_s) - a2) + a3 > p_b{}^{max} \end{cases}$$

$$p_z = p_b$$

where

$B_c$, $B_h$, $B_s$ – biomass of cod, herring and sprat, respectively,
$A1$, $A2$, $A3$, $a1$, $a2$, $a3$, $p_b{}^{max}$ – parameters,
$\rho_h$ – vulnerability of herring to cod predation,
$\mathrm{Th}$ – tangent hyperbolic function.

The constrains have been imposed in order to retain $pp \leq 1$ ($p$ may be greater than 1) and prevent too high consumption of zooplankton and benthos. Now Andersen & Ursin's preference $G_{ij}$ becomes

$$G_{ij} = p_{ij}\, \rho_{ij}\, g_{ij}.$$

*Mortality due to starvation*

Andersen & Ursin (1977) incorporated density dependent starvation mortality of the larval stages into their model. Here, the starvation mortality formula was developed on the basis of Ivlev's (1955) experiments with starving fish. Ivlev examined

Table 1. Time (days) of death of 50% of bream and sheatfish fed by reduced ration $r$, with respect to sustained one $Rs$ (Ivlev, 1955).

| $r/Rs$ | Bream | Sheatfish |
|--------|-------|-----------|
| 0      | 34    | 46        |
| 0.1    | 51    | 76        |
| 0.2    | 73    | 89        |
| 0.4    | 94    | 116       |
| 0.75   | 117   | 142       |
| 1.0    | 126   | 151       |

the time of death of 50% of fish fed by a ration, $r$, reduced with respect to sustained one, $Rs$ (Table 1). His results can be approximated by

$$t_{50\%} = b1 - \exp(-b2\, r/Rs)$$

where $b1$ and $b2$ are parameters. Further, Ivlev states that $t_{50\%}$ increases linearly with fish age

$$t_{50\%}(t) = (b1 - \exp(-b2\, r/Rs))(t + 1).$$

From the Andersen & Ursin theory, it results that

$$r/Rs = f/fs$$

where $f$ and $fs$ are the actual and sustained feeding levels respectively. As $fs$ fulfills $dw/dt=0$, then

$$r/Rs = vhw^{-1/3}f/k.$$

Let's assume that the fraction, $S$, of death due to starvation in time $\Delta t$ is proportional to the length of that interval in power $u$. Then

$$S/0.5 = (\Delta t/t_{50\%})^u$$

and as

$$S = 1 - \exp(- \overline{MS}\, \Delta t)$$

we have the mean in the interval $\Delta t$ coefficient of starvation mortality, $\overline{MS}$

$$\overline{MS} = \begin{cases} 0 & \text{for } f \geq fs, \\[2ex] -\dfrac{1}{\Delta t} \ \ln\left(1 - 0.5\left(\dfrac{\Delta t}{(b1 - \exp(-b2\ vhw^{-1/3}f/k))(t+1)}\right)^u\right) & \\ & \text{for } f < fs \text{ and } \Delta t < 2^{1/u}\,t_{50\%}, \\[2ex] \infty & \text{for } f < fs \text{ and } \Delta t \geq 2^{1/u}\,t_{50\%}, \end{cases}$$

where $2^{1/u}\,t_{50\%}$ is the time of the starvation death of all the fish.

*External variables*

The model presented has been applied in Sub-divisions 25-29S of the Baltic Proper to assess predator-prey interactions and to analyze different exploitation patterns. Fig. 2 illustrates the simulated trophic levels.
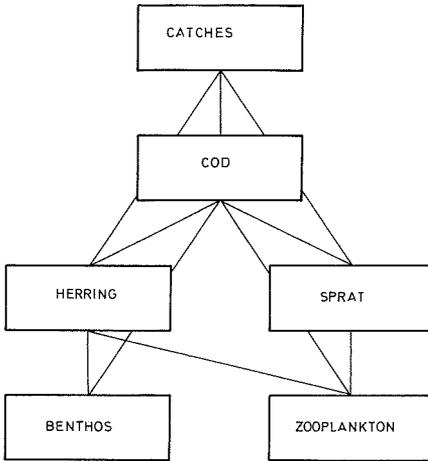


Fig. 2. Simulated trophic levels in Sub-divisions 25-29S of the Baltic.

   To have a complete model, the author has attempted to develop submodels of fish recruitment and fishing mortality. However, no distinct relationship was found between cod recruitment and spawning stock biomass and data on salinity, oxygen conditions, water temperature on the spawning ground collected by the Sea Fisheries Institute. Similarly, mean fishing mortality of cod and herring appeared to be only slightly dependent on fishing effort (determined as the ratio of the total catch to the catch per unit of effort of a selected vessel) and exploited stock biomass. Thus, recruitment and fishing mortality were treated as external variables. Their values were taken from VPA results (Anon, 1986 a,b). The recruitment estimates were then increased by multiplying them by a constant factor to compensate for high grazing mortality of the youngest fish. In the case of sprat, different factors were used for the periods 1974-77 and 1978-84 to reflect low and high predator biomass in these periods. To reflect fishing mortality of the pre-recruit fish, mean long-term partial recruitment coefficients were used.

Zooplankton and benthos were also treated as external variables. Their mean yearly values for 1974-79 (Table 2) were estimated by Horbowy & Kuptel (1980 based on the Sea Fisheries Institute's data on zooplankton and benthos distribution in the Gulf of Gdansk and the estimate of long-term production of zooplankton and long-term benthos biomass (Thurow, 1978)). For the 1980-84 period, average

Table 2. Mean yearly biomass ($10^6$ tons) of zooplankton and benthos used in the model.

| Year | 1974 | 1975 | 1976 | 1977 | 1978 | 1979 | 1980-84 |
|------|------|------|------|------|------|------|---------|
| Zooplankton | 4.4 | 4.4 | 4.8 | 4.0 | 5.4 | 5.1 | 4.7 |
| Benthos | 2.8 | 2.9 | 3.0 | 2.7 | 3.2 | 3.3 | 3.0 |

values were used as there is a lack of appropriate yearly data. Each month, a new biomass of zooplankton and benthos is introduced into the model on the basis of their monthly distribution in the Gulf of Gdansk (Horbowy & Kuptel, 1980); the weight of the individuals present remains constant.

*Parameter values*

The parameter values are presented in Table 3. The food preference parameters for cod were determined on the basis of cod stomach contents data (Załachowski, in press); these data were also submitted to the Working Group on Multispecies Assessments of Baltic Fish. For the $\eta$, $\sigma$ and $\rho$ values, the method of Ursin (1973) slightly modified by Horbowy (1982) was used. Parameters $A1$, $A2$, $A3$, $a1$, $a2$, $a3$ were adjusted so as to give simulated $p$ values close to the observed (Fig. 3). In order to determine the observed $p$ values the $\rho$ estimates for each year were obtained by the method cited above. Next it was assumed that the variance in the $\rho$ values is caused by the $p$ values contained in them, so the observed $p$'s were estimated from the formula

$$p_{ij}^{y} = \rho_{ij}^{y} \rho_{ij}$$

where $\rho$ is mean vulnerability for the 1977-84 period and y denotes a year. The $\eta$, $\sigma$ and $\rho$ values for herring and sprat were assumed.

To determine growth parameters, von Bertalanffy's equations were fitted to weight-at-age data (Anon., 1986a,b). Weight-at-age estimates for herring and sprat
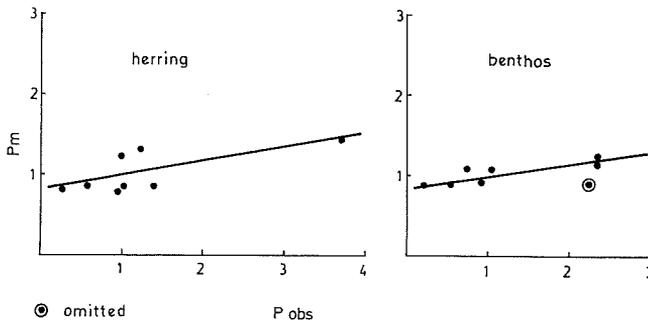


Fig. 3. Modeled prey biomass-dependent preference index, $p_m$, versus observed one, $p_{obs}$, for two cod preys: herring and benthos.

Table 3. Values of parameters used in the model.

| Parameter | Age group | Cod | Herring | Sprat |
|---|---|---|---|---|
| $v$ | | 0.3 | 0.3 | 0.3 |
| $h$ | | 18.7 | 27.0 | 10.2 |
| $k$ | | 0.023 | 1.3 | 0.93 |
| | 0 | 27 | 225 | 20 |
| | 1 | 20 | 59 | 8 |
| | 2 | 50 | 97 | 16 |
| | 3 | 74 | 121 | 28 |
| $q$ | 4 | 169 | 161 | 56 |
| | 5 | 600 | 231 | 86 |
| | 6 | 1750 | 341 | 200 |
| | 7 | 4400 | 451 | 594 |
| | 8 | 11000 | 501 | – |
| $\eta_{cod}$ | | 3.6 | – | – |
| $\eta_{herring}$ | | 4.15 | – | – |
| $\eta_{sprat}$ | | 4.55 | – | – |
| $\eta_{benthos}$ | | 6.1 | 5.9 | – |
| $\eta_{zooplankton}$ | | 5.0 | 5.9 | 5.6 |
| $\sigma_{cod}$ | | 1.05 | – | – |
| $\sigma_{herring}$ | | 0.76 | – | – |
| $\sigma_{sprat}$ | | 1.0 | – | – |
| $\sigma_{benthos}$ | | 0.25 | 0.02 | – |
| $\sigma_{zooplankton}$ | | 0.15 | 0.02 | 0.15 |
| $\rho_{cod}$ | | 0.5 | – | – |
| $\rho_{herring}$ | | 0.6 | – | – |
| $\rho_{sprat}$ | | 1.0 | – | – |
| $\rho_{benthos}$ | | 0.42 | 1.0 | – |
| $\rho_{zooplankton}$ | | 0.046 | 1.0 | 1.0 |
| $A1$ | | 0.36 | | |
| $A2$ | | 4.4 | | |
| $A3$ | | 1.2 | | |
| $a1$ | | 2.4 | | |
| $a2$ | | 0.25 | | |
| $a3$ | | 0.8 | | |
| $M1$ | | 0.25 | 0.15 | 0.15 |
| $b1$ | | 1.1 | 1.1 | 1.1 |
| $b2$ | | 0.33 | 0.33 | 0.33 |
| $u$ | | 2.0 | 2.0 | 2.0 |

in Sub-divisions 25-29S were determined as the weighted by numbers mean weight-at-age of appropriate populations (herring in Sub-divisions 25-27 and 28-29S, and sprat in Sub-divisions 25, 26 + 28 and 27 + 29S). Next, the $v$ value taken from Jobling (1982) was used to calculate

$$hf_i = h\phi_i/(\phi_i + q_i NS_i) = H/v$$

for $i$ belonging to a species and $H$ being the anabolism coefficient in von Bertalanffy's equation. The above simultaneous equations served for the estimation of $q_i$ values. The number of unknown parameters ($q_i$ and $h$) is greater by 1 than the number of equations, so $h$ was chosen in such a way as to give the best correspondence of the observed and simulated in the model growth of fish.

The values of $b1$ and $b2$ were determined on the basis of Ivlev's (1955) experiments (Table 1). $M1$ was adjusted so as to give $M$ for adult fish similar to the values assumed by the Baltic Working Groups.

## Results and Discussion
### Reliability of the model
The mean relative differences between the simulated and observed catches of cod, herring and sprat were 10, 9 and 12%, respectively (Table 4). At least part of that difference is caused by the mean long-term partial recruitment coefficients used in the model. For example, employing actual partial recruitment coefficients for cod in 1977 would reduce the difference for that year from –27% to –7%.

Table 4. The relative difference between the catches (in weight) determined by the multispecies model and the observed catches from Working Group reports for 1974-1984 period (in %).

| Year | Cod | Herring | Sprat |
|---|---|---|---|
| 1974 | –1 | –13 | –13 |
| 1975 | 18 | –6 | 3 |
| 1976 | –14 | 14 | 6 |
| 1977 | –27 | 5 | 8 |
| 1978 | –1 | 12 | –11 |
| 1979 | 10 | 6 | –11 |
| 1980 | –6 | 10 | –23 |
| 1981 | –15 | –12 | –14 |
| 1982 | –4 | 10 | –17 |
| 1983 | 6 | 9 | 2 |
| 1984 | 5 | –5 | 21 |
| Mean of absolute values | 10 | 9 | 12 |

Table 5. The correlation coefficients between catch at age in numbers estimated by the model and observed one in 1974-1984.

| Age group | Cod | Herring | Sprat |
|---|---|---|---|
| 0 | – | 0.23 | –0.05 |
| 1 | 0.33 | 0.40 | 0.89 |
| 2 | –0.02 | 0.59 | 0.85 |
| 3 | 0.56 | 0.79 | 0.96 |
| 4 | 0.95 | 0.88 | 0.94 |
| 5 | 0.92 | 0.72 | 0.93 |
| 6 | 0.92 | 0.78 | 0.89 |
| 7 | 0.93 | 0.97 | – |

A comparison of the age composition of cod, herring, and sprat catches, calculated by means of the model, with the observed age composition is presented in Table 5. Correlation coefficients between observed and calculated catches are high in most cases. Greater deviations may be observed mostly in partially recruited age groups. For cod, this may be seen in age groups 1 and 2, for herring – in age groups 0 and 1, for sprat – in age group 0. These differences are the result of causes discussed above – the use of mean long-term partial recruitment coefficients. As a re-
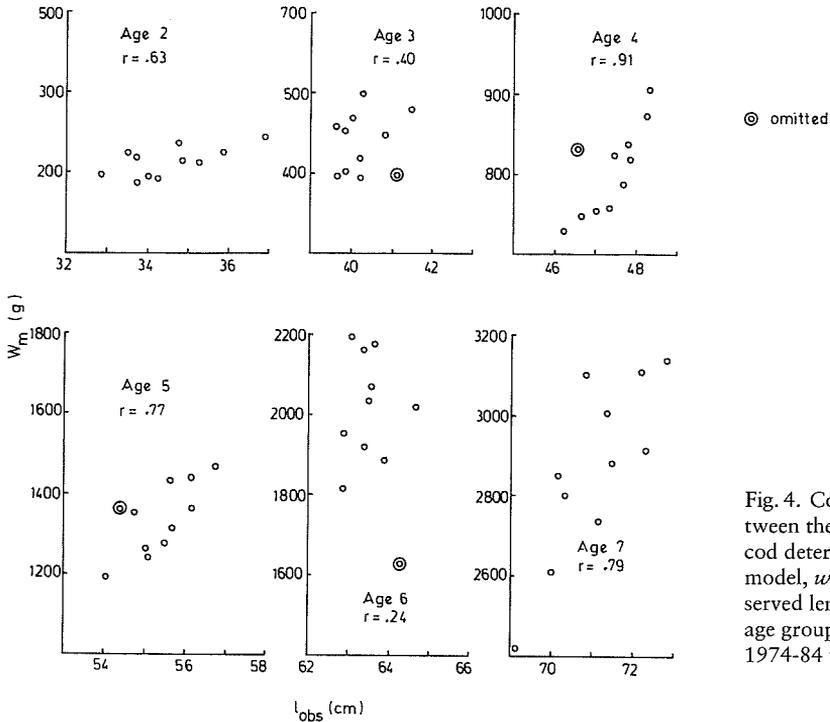
Fig. 4. Correlation between the weight of cod determined by the model, $w_m$, and observed length, $l_{obs}$, by age groups 2-7 in 1974-84 years.

sult, there is a certain error in those years, in which deviations of the coefficients from their mean values are quite large.

Weight of cod by age groups simulated in the model is in fairly good agreement with cod lengths observed in the catches (Fig. 4). Observed length (Kosior, pers. communication) instead of observed weight was used for comparison because of its better availability and greater accuracy. The highest correlation coefficients between calculated and observed values were obtained for cod age groups 4, 5 and 7 (about 0.8), lower for age groups 2 and 3 (0.63 and 0.40 respectively). Cod age groups 2 and 3 are not fully recruited to the exploitable stock so only larger specimens from these groups are caught. This may be the cause of poor correlation between their simulated and observed growth. The model did not reflect the growth of the cod age group 6. The reason for that may be low variation in the observed values.

A comparison of growth of herring and sprat calculated from the model with the observed growth is somewhat difficult since the model use simulated herring and sprat stocks from Sub-divisions 25-29S while available data refer to growth observed in actual stocks. Grygiel (1979) presented the mean weight of sprat in the southern Baltic by age groups for the 1974-1977 period. When these data were compared with the values obtained from the model, a rather good relationship was obtained (Fig. 5). The adequacy of the herring growth equation used in the model may be argued on the basis of Horbowy (1983). Using a herring growth equation

Fig. 5. Correlation between the modeled, $W_m$, and observed, $W_{obs}$, weight of sprat by age groups 0-5 in 1974-1977 years.
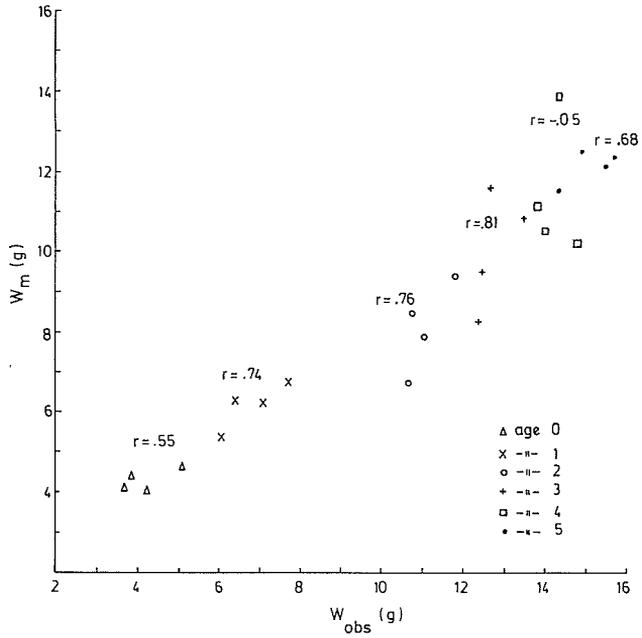


Fig. 6. Correlation between the share of sprat, herring and zooplankton + benthos in the cod's food determined on the basis of the model, $P_m$, and observed share, $P_{obs}$, by cod's age groups 2-6 in 1977-1984 years.
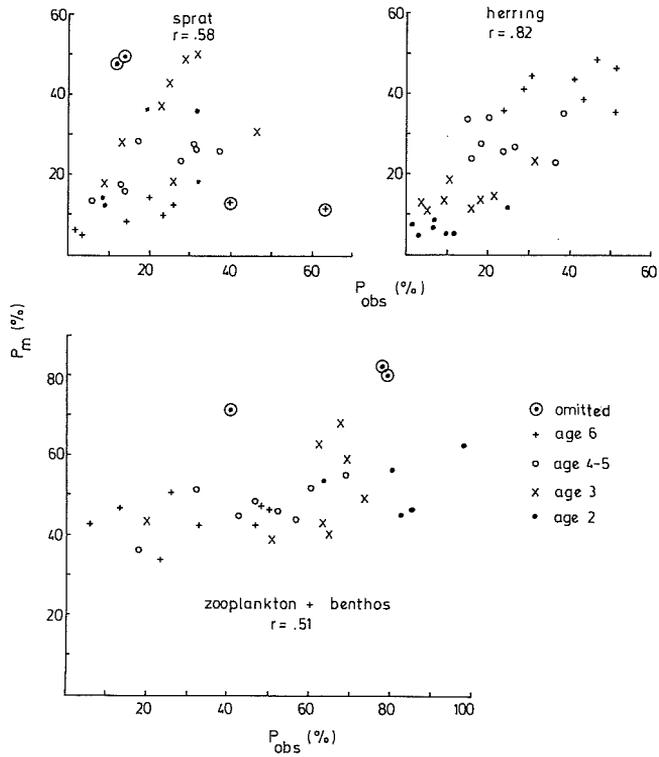
similar to that used here, the author obtained good comparability between the calculated length and the observed.

The last criterion of the model's reliability consisted of a comparison of the simulated and observed species composition of the food of cod. Only the food of cod was considered since the food of herring and sprat was treated in the model in a very general way (zooplankton as a whole and benthos as a whole). The observed composition of cod food (Załachowski, in press) is presented by 5- and 10-cm length classes. On the other hand, the model is based on the use of age groups and all calculations are made for them. Thus, to enable a comparison of the calculated food composition with the observed, age groups were assigned to all length intervals from the data of Załachowski. This procedure resulted in a certain error in the obtained data observed by age group since individual age groups did not correspond exactly to the length classes according to which Załachowski classified his data. Nevertheless the correlation between the simulated and observed food composition of cod split into herring, sprat, and zooplankton + benthos (Fig. 6) was fairly satisfactory. It is worth noting that the model reflects relatively well changes in the share of sprat in the food of individual cod age groups and – to a lesser degree – the share of zooplankton + benthos in the food of age groups 3 and 4-5 in consecutive years. The model did not reflect the variance of the observed share of herring in the food of various age groups of cod. This may have been caused by a lower variance in this share when compared with sprat and zooplankton + benthos.

*Stock dynamics in the 1974-1984 period*

Biomass values simulated in the model for cod, herring, and sprat stocks in the 1974-84 period are shown in Fig. 7. For comparison, biomass estimates of these species made by the Baltic multispecies Working Group (Anon., 1988) are presented as well. All presented values refer to 1 January. Herring biomass estimates from the model are very close to the multispecies Working Group values while the simulated biomass of sprat exhibits a similar trend to the multispecies Working Group estimates with an increasing difference from 1981-84. The MSVPA values of predation mortality were in the range of 1.0-1.8 for many age groups of sprat from Sub-division 25. This is about 3 times higher than the model estimates. The biomass estimates of cod also show a similar trend to the MSVPA values. However, MSVPA values are about 50% greater than the model estimates. This difference was primarily caused by the cod's weights-at-age which, in the MSVPA, are 200-50% higher for the 2-4 age groups respectively than those simulated in the model. These age groups constitute about 50% of cod biomass and the weights-at-age used in the MSVPA are weights-at-age in the catch, which may result in overestimation of MSVPA biomass.

The consumption of herring-like fish by cod in 1974-84 estimated by the model was, on average, about 550 thous. tons (410 to 760 thous. tons (Table 6)). This figure included, on the average, 210 thous. tons of herring (120-290 thous. tons range) and 335 thous. tons of sprat (190-540 thous. tons range). In the 1976-79 period, the consumption of sprat by cod kept decreasing, being compensated for by increasing consumption of benthos (as high as 900-1000 thous. tons). The main reason for
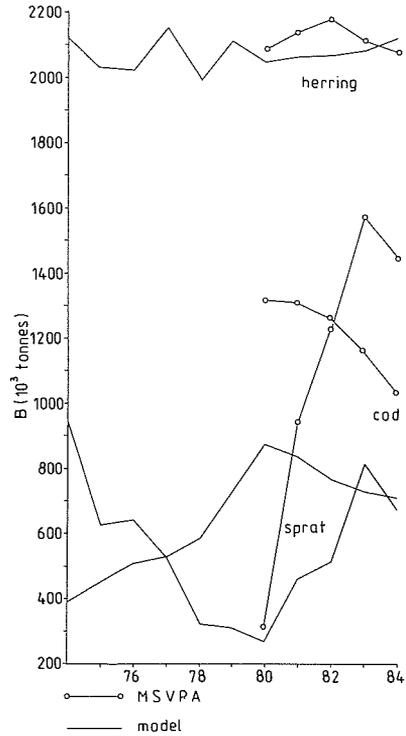
Fig. 7. Biomass, *B*, of cod, herring and sprat simulated in the model and biomass estimated by multispecies *VPA* (all values refer to 1 January, 0 age group is excluded).

this decrease of sprat consumption was the abundance of its generations in the years 1976-79 which directly influenced the low abundance of the youngest age groups on which cod usually prey. It does not seem that the increase in biomass of cod (from 600 to 900 thous. tons in 1978-83 (Fig. 7)) could have had a decisive impact

Table 6. The biomass consumed by cod, BC (thous. tons), and predation mortality, *M2*, by species estimated by the model.

| Year | Herring BC | Herring M2 | Sprat BC | Sprat M2 | Young cod BC | Young cod M2 | Zooplankton BC | Benthos BC |
|------|------|------|------|------|------|------|------|------|
| 1974 | 117 | 0.11 | 311 | 0.44 | 5 | 0.06 | 135 | 427 |
| 1975 | 152 | 0.13 | 333 | 0.52 | 7 | 0.09 | 158 | 438 |
| 1976 | 159 | 0.13 | 273 | 0.50 | 9 | 0.09 | 236 | 531 |
| 1977 | 219 | 0.20 | 203 | 0.55 | 11 | 0.09 | 263 | 618 |
| 1978 | 228 | 0.19 | 186 | 0.69 | 9 | 0.07 | 236 | 895 |
| 1979 | 285 | 0.25 | 217 | 0.84 | 12 | 0.10 | 235 | 1037 |
| 1980 | 282 | 0.23 | 340 | 0.78 | 15 | 0.12 | 234 | 927 |
| 1981 | 241 | 0.21 | 406 | 0.77 | 14 | 0.10 | 208 | 814 |
| 1982 | 216 | 0.17 | 543 | 0.64 | 11 | 0.08 | 150 | 650 |
| 1983 | 219 | 0.17 | 514 | 0.69 | 10 | 0.10 | 150 | 612 |
| 1984 | 215 | 0.16 | 358 | 0.59 | 10 | 0.09 | 182 | 591 |
| Mean | 212 | 0.18 | 335 | 0.63 | 10 | 0.09 | 199 | 685 |

Table 7. Mean biomass consumed by cod (thous. tons) by age groups in 1974-1984 estimated by the model.

| Cod age group | Prey species | | | |
|---|---|---|---|---|
| | Herring | Sprat | Benthos | Zoo-plankton |
| 0 | 0 | 0 | 13 | 90 |
| 1 | 3 | 25 | 115 | 84 |
| 2 | 21 | 83 | 180 | 20 |
| 3 | 47 | 125 | 164 | 4 |
| 4 | 52 | 70 | 110 | 1 |
| 5 | 39 | 23 | 56 | 0 |
| 6 | 24 | 7 | 26 | 0 |
| 7 | 14 | 2 | 12 | 0 |
| 8+ | 12 | 0.5 | 9 | 0 |

Table 8. Biomass (thous. tons) of herring and sprat consumed by cod in 1980-1984 estimated by the multispecies VPA (Anon., 1988).

| Year | Herring 25-29S | Sprat 25, 26+28 |
|---|---|---|
| 1980 | 775 | 187 |
| 1981 | 856 | 664 |
| 1982 | 810 | 821 |
| 1983 | 677 | 943 |
| 1984 | 583 | 663 |

on the low recruitment of sprat. This argument is supported by the fact that the numbers of recruited herring, which are also eaten intensively by cod, did not undergo great fluctuations. In the 1980-1984 period, a large increase in the consumption of sprat, thus, reflecting an increase in its biomass, was observed. This was accompanied by a decrease in benthos consumption.

Cod from age groups 2-4 eat, on average, 280 thous. tons of sprat. This constitutes 83% of the sprat biomass consumed by all predators (Table 7). Herring are mostly consumed by cod age groups 3-5 and the amount consumed is 140 thous. tons, which constitutes 65% of herring biomass lost to predation.

Let us also compare the consumption by cod calculated by means of the model with multispecies VPA estimates made in Anon. (1988), (Table 8). The cod's consumption of herring assessed by the Baltic multispecies Working Group is about 3 times greater than the model estimates (Table 6) while cod's consumption of sprat exceeds the model values by about 50%. The MSVPA simulations are based on the annual consumption by cod calculated using the evacuation rate for North Sea cod (24 hours). However, *in situ* estimation of the evacuation time of sprat from cod stomachs in Sub-divisions 25 indicated a period of 60-70 hours (Anon., 1988). Applying this value in the calculations, would reduce the biomass of sprat consumed by cod estimated in MSVPA by about a factor of 3. Taking into account in MSVPA, sprat from Sub-divisions 27 and 29S could produce a value for sprat biomass eaten by cod, which is close to the model estimates. Assuming that the evacuation time for herring in cod stomachs is similar to that for sprat, then the herring biomass consumed by cod assessed by MSVPA would also decrease by a factor of about 3 and would be very close to the model estimates. Some differences between the estimates of cod consumption may be caused by basing the model on Polish stomach content data only while the MSVPA runs employ both Polish and USSR data which are different.

The entire sprat stock, 0-1 age groups of herring and the 0 age group of cod sustain the heaviest predation by cod (Table 9). The other fish are consumed to a small degree.

Table 9. Mean (1974-1984) predation mortality coefficient, $M2$, of herring, sprat and young cod by age groups estimated by the model.

| Age group | Herring | Sprat | Young cod |
|---|---|---|---|
| 0 | 0.28 | 0.69 | 0.18 |
| 1 | 0.24 | 0.71 | 0.08 |
| 2 | 0.13 | 0.52 | 0.02 |
| 3 | 0.08 | 0.40 | 0 |
| 4 | 0.06 | 0.32 | 0 |
| 5 | 0.04 | 0.28 | 0 |
| 6 | 0.04 | 0.25 | 0 |
| 7 | 0.04 | – | 0 |

Table 10. Mean feeding level, $f$, of cod, herring and sprat in 1974-1984 estimated on the basis of multispecies model.

| Year | Cod | Herring | Sprat |
|---|---|---|---|
| 1974 | 0.94 | 0.66 | 0.74 |
| 1975 | 0.93 | 0.66 | 0.76 |
| 1976 | 0.93 | 0.67 | 0.81 |
| 1977 | 0.91 | 0.63 | 0.83 |
| 1978 | 0.92 | 0.70 | 0.89 |
| 1979 | 0.91 | 0.69 | 0.91 |
| 1980 | 0.90 | 0.67 | 0.89 |
| 1981 | 0.90 | 0.67 | 0.87 |
| 1982 | 0.91 | 0.67 | 0.84 |
| 1983 | 0.92 | 0.66 | 0.82 |
| 1984 | 0.92 | 0.66 | 0.83 |

The mean feeding level of cod in the 1974-1984 period (Table 10) was quite stable and estimated to be 0.90-0.94. This indicates that the low biomass of sprat in 1977-1980 did not significantly affect feeding conditions for cod, which compensated for this decline by increasing their consumption of zooplankton and benthos.

The feeding level of herring was also quite stable, ranging from 0.63 to 0.70. The large decline in sprat biomass in 1977-1980 resulted, in turn, in a considerable increase in its feeding level from 0.75 to 0.9, signifying an increase of its asymptotic weight by about 70%. These estimates of feeding level reflect trends in its changes rather than absolute values, which are difficult to assess.

The mean value of the natural mortality coefficient due to starvation in the 1974-1984 period was 0.04 and 0.02 for age group 0 of herring and sprat, respectively. Natural starvation mortality of the other herring and sprat age groups was estimated to be in the range of 0-0.003. The value of the presented estimates is small because it was based on parameters determined on the basis of Ivlev (1955) for bream and sheatfish.

*Various patterns of stock exploitation*

After verifying the model, it was used for the simulation of several patterns of stock exploitation. The state of stocks and catches were analysed at an equilibrium point attained by the system about 10 years after an assumed pattern of exploitation has started. Fishing mortality of cod was set at different levels between 40 and 190% of a long-term mean (1974-84) while fishing mortality of herring-like fish was set to between 70 and 130% of the appropriate mean. Recruitment to the stock was simulated by its mean from 1974-84 years.

The highest total catches of the three species together were assessed at about 665 thous. tons and attained when fishing mortality of cod equalled 190% and herring-like fish – 130% of their long-term means (Fig. 8). However, such an intensive exploitation of cod would result in a decline of its spawning stock to a level of about 200 thous. tons, which might be unfavourable with regard to spawning success. For
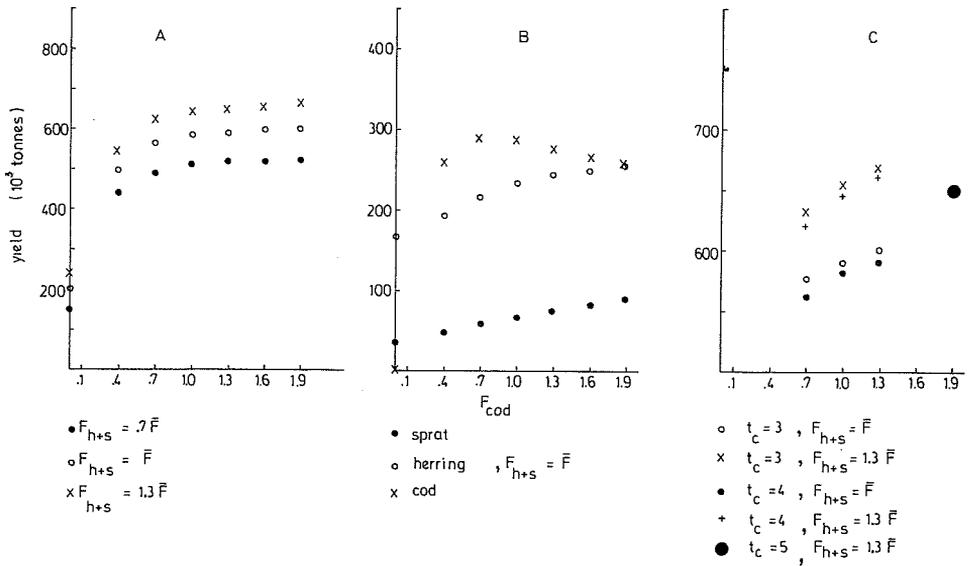
Fig. 8. A. Total catches for different fishing mortality of cod $F_{cod}$, and herring-like fish, $F_{s+h}$. B. Catches by species for different $F_{cod}$. C. Total catches for different $F_{cod}$ and $F_{h+s}$, and age of full capture of cod, $t_c$ (the unit of fishing mortality is the long-term mean fishing mortality).

this reason the variant according to which cod fishing mortality should increase by 60% should be considered to give maximum yield. This enables a catch of 660 thous. tons of fish, including 265 thous. tons of cod and 395 thous. tons of herring and sprat. Such catches would be higher by 15 thous. tons than those attained at an exploitation intensity of cod equal to the long-term mean. At the same time, the cost of cod catches would increase significantly because of the great decline of its biomass and related drop in the catch per effort. The simulations also indicate the overfishing of cod. A decrease of fishing intensity to 70% of its long-term mean would enable a slight increase of cod catches and a concomitant reduction of costs. Other simulations were made in order to assess the impact of both abandoning fishing operations for cod and the elimination of cod from the ecosystem on stocks and catches. In the first case, total catches dropped considerably (to 200 thous. tons). This figure included 164 thous. tons of herring and 37 thous. tons of sprat.

The problem of the state of stocks after eliminating the cod population is far from simple since, as the result of the lack of natural mortality due to predation $M2$, natural mortality $M1$ would probably increase (the predator eliminates weaker and diseased individuals). We are unable to estimate this change.

Employing in the calculations the hitherto used values of $M1$, the total catch after eliminating cod stock and maintaining fishing intensity for herring and sprat at unchanged levels equalled 510 thous. tons (herring – 270 thous. tons, sprat – 230 thous. tons). However, due to their overabundance, these fish would be small, weights of sprat would not exceed 6g, weights of herring – 40g. Increasing fishing mortality for herring-like fish up to 3 times the mean value would allow for catch-

ing 920 thous. tons of fish (herring – 560 thous. tons, sprat – 360 thous. tons) of normal size.

Assuming that $M1$ increases to the currently assumed value of total natural mortality for adults ($M = 0.2$ for herring, $M = 0.5$ for sprat) then by increasing fishing mortality of herring and sprat 3 times, we would have a catch of 700 thous. tons (500 thous. tons of herring, 200 thous. tons of sprat).

The actual catch after eliminating cod would probably be contained somewhere within these levels, determined by extreme values of $M1$. However, these considerations do not take into account positive effects of predator presence (e.g. a decrease in the fluctuations of prey population biomass, elimination of weaker and diseased individuals).

The next simulation involved the influence of a change of the age of full capture of cod on the catches attained, with the fishing mortality for herring-like fish equal to the long-term mean and 30% higher than the mean, and employing various levels of fishing mortality for cod (Fig. 8). The most favourable results were obtained when the age of full capture of cod was reduced from the current 4 to 3 years and fishing mortality for cod, herring and sprat was increased by 30%. The catch attained at this variant would be about 670 thous. tons (230 thous. tons of cod and 440 thous. tons of sprat and herring), i.e. higher by 10 thous. tons than in the best variant maintaining the present age of full capture of cod. A further increase in fishing mortality of cod would result in a decline of the biomass of its spawning stock below 200 thous. tons. A variant involving an increase of the age of full capture of cod to 5 years and a simultaneous large (90%) increase of its fishing mortality (intensive catch of older fish, feeding mainly on herring-like fish) turned out to be unfavourable. There were two reasons for this. First, a greater part of the consumed biomass of sprat and herring is eaten by cod in age groups 2-5 (Table 7). Second, this variant does not lead to a sufficient decrease of cod biomass due to their being caught so late.

The simulations carried out point to a moderate sensitivity of total catches to changes in fishing intensity of cod ranging from 40 to 190% of their long-term mean. Their increase is about 70-120 thous. tons, a result of an increase in cod catches by about 35 thous. tons. Only the total elimination of cod has a visible impact on the yield obtained. Although the biomass of herring and sprat consumed by cod seems moderate it consists mainly of young fish. As a result, cod eliminates about 50% of sprat in age group 0 and 25% of the same age group of herring.

The dependence of the biomass of the herring-like fish on the biomass of cod (Fig. 9) resembles a power relationship (linear on the logarithmic scale). An increase in cod stock biomass $\alpha$ times results in a decrease of herring and sprat biomass by about $\alpha^g$ times. The influence of herring and sprat biomass on cod biomass is much smaller in the biomass range taken into account here. A decrease in herring and sprat stock by 10% brings about a decline in cod biomass by about 1% and is practically not reflected in the catches.
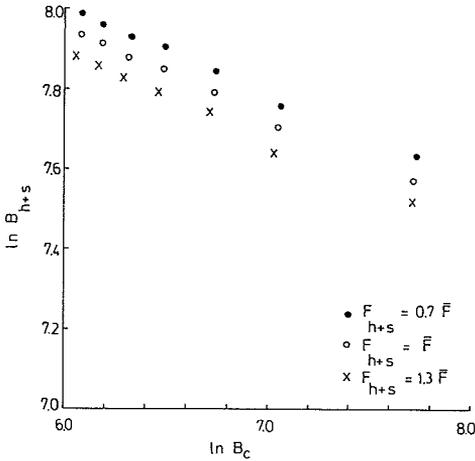
Fig. 9. The relationship between herring-like fish biomass, $B_{h+s}$, and cod biomass $B_c$, for three levels of herring and sprat fishing mortality, $F_{h+s}$.

## Discussion of modifications tested

Let us analyse the advisability and effect of the modifications introduced into the Danish model on the basis of the results of simulations and literature. The direct introduction of the abundance of fish competing for food, $NS$, to the denominator of the formula for feeding level is justified by the experiments of Houde (1975, 1977). He found that the growth rate and survival of sea bream, bay anchovy and lined sole larvae were negatively correlated with population density. The dependence of growth on population density resembled the hyperbolic function used here to describe feeding level. In addition, Horbowy (1983) presented a model of Baltic herring growth, in which relating feeding level to the number of fish made it possible to reflect the observed growth.

The influence of the introduction of a food preference coefficient dependent on the biomass of prey, $p$, may be well seen by comparing the growth of cod age groups 4 and 5, obtained from two models (Fig. 10). A sudden decline in the sprat stock biomass in 1977-1979 (in Fig. 7 the lowest sprat biomass is in 1980 but it does not include the 0 age group which was very abundant in that year) was immediately reflected in the growth of these two age groups calculated with the help of the unmodified model. In the case of the modified model, cod compensated for the scarcity of sprat by increasing consumption of zooplankton and benthos. As a result of this, growth of cod was similar to that observed. Feeding on sprat is much less important for cod in age groups 6 and 7 and for these groups, both models give a qualitatively similar picture of predator growth to that observed. As a result, the modified form of $f$ and the introduction of coefficient $p$ led to a much higher correlation between calculated cod growth and that observed (Table 11). The present model also better reflects the growth of sprat (Table 11).

The accuracy of the formula for natural mortality due to starvation introduced here may be discussed only on the basis of literature as appropriate data are not available. Ursin (1967) determined the catabolism coefficient for *Lebistes reticula-*
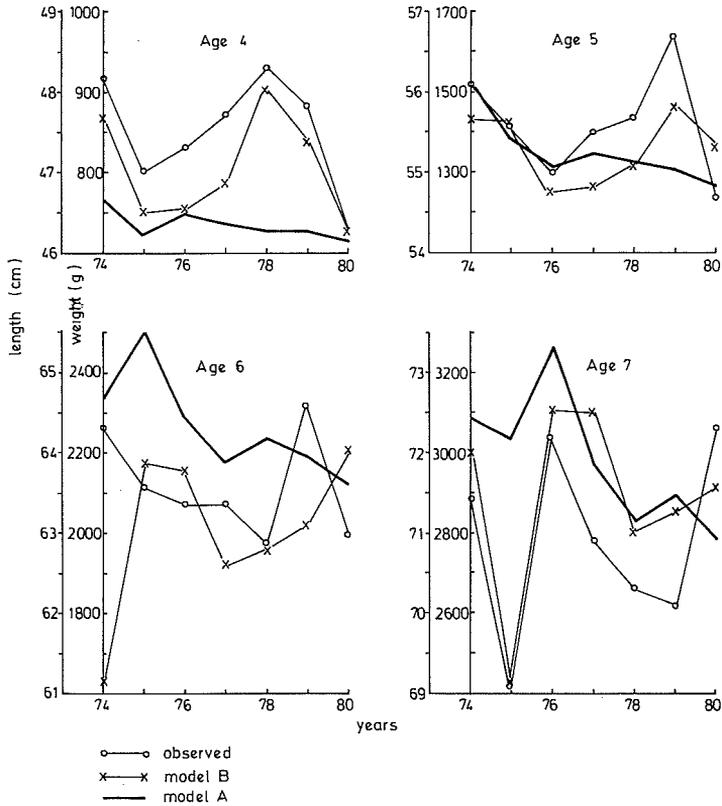
Fig. 10. Cod growth in weight simulated in the unmodified model (A), in the modified model (B), and the observed growth of cod in length in 1974-1980 years.

o——o observed
x——x model B
——— model A

*tus*, observing that until the fish lost 20% of their weight, mortality was low and then rapidly increased. This seems to be in agreement with *MS* treated as a function of $\Delta t$, which first increases slowly and then rapidly. Laurence (1974) investigated the growth and mortality of haddock larvae depending on the amount of food. He obtained a high correlation between growth and survival rate of larvae and amount of food available to one larva, $\phi/N$. The dependence of mortality on $\phi/N$ is similar to the relationship between presented here for the functional form of *MS* and $\phi/N$. Mills (1982) analysed factors influencing the mortality and growth of dace larvae.

Table 11. The correlation of the fish growth determined by the unmodified model (a) and modified model (b) with the observed growth.

| Species | | 1 | 2 | 3 | 4 | 5 | 6 | 7 |
|---|---|---|---|---|---|---|---|---|
| | | | | | Age group | | | |
| Cod | a | — | −0.19 | 0.55 | 0.55 | 0.40 | 0.20 | 0.18 |
| | b | — | 0.63 | 0.40 | 0.91 | 0.77 | 0.24 | 0.79 |
| Sprat | a | −0.57 | −0.39 | 0.36 | 0.88 | 0.54 | — | — |
| | b | 0.74 | 0.76 | 0.81 | −0.05 | 0.68 | — | — |

It turned out that growth rate was smaller and mortality greater in tanks with a greater number of larvae. Changes in mortality due to the abundance of larvae were similar to changes of *MS* as a function of *N*. The investigations carried out by Werner & Blaxter (1982) on the influence of food on the growth and survival rate of herring larvae showed that both processes depend on the amount of food and changes in mortality were qualitatively similar to the changes of *MS*.

## Acknowledgements

## References

*Andersen, K.P., Ursin, E.* 1977. A multispecies extension to the Beverton and Holt theory of fishing with accounts of phosphorus circulation and primary production. – Meddr Danm. Fisk- og Havunders. N.S. 7: 319-435.

*Anon.*, 1981. Report of the *ad hoc* Working Group on multispecies assessment in the Baltic. – ICES C.M. 1981/J:34.

*Anon.* 1986a. Report of the Working Group on the assessment of the demersal stocks in the Baltic. – ICES 1986/Assess.: 21.

*Anon.* 1986b. Report of the Working Group on the assessment of the pelagic stocks in the Baltic. – ICES 1986/Assess.: 20.

*Anon.* 1988. Report of the Working Group on multispecies assessments of Baltic fish. – ICES 1988/Assess.: 1.

*Grygiel, W.* 1979. Wzrost szprota poludniowego Baltyku. (The growth of sprat in the southern Baltic). – *In:* Z biologii ryb Baltyku. Studia i materialy. Ser. B/44.

*Horbowy, J.* 1982. The estimation of parameters of predator-prey preference function for Baltic cod. – ICES 1982/J:28.

*Horbowy, J.* 1983. The modeling of the coastal spring herring growth and modified yield per recruit curve. – ICES 1983/J:5.

*Horbowy, J., Kuptel, M.* 1980. Use of a multispecies model to assess Baltic stocks and forecast catches. – ICES 1980/J:15.

*Houde, E.D.* 1975. Effects of stocking density and food density on survival, growth and yield of laboratory-reared larvae of sea bream *Archosargus rhomboidalis* (L), (Sparidae). – J. Fish. Biol. 7: 115-127.

*Houde, E.D.* 1977. Food concentration and stocking density effects on survival and growth of laboratory-reared larvae of bay anchovy *Anchoa mitchili* and lined sole *Achirus lineatus*. – Marine Biology. 43: 333-341.

*Ivlev, V.S.* 1955. Eksperimentalnaja ekologia pitanija ryb. (Experimental ecology of fish feeding). – Naukova dumka. Kiev.

*Jobling, M.* 1982. Food and growth relationship of th cod, *Gadus morhua* L., with special references to Balsfjorden, north Norway. – J. Fish. Biol. 21: 357-371.

*Laurence, G.C.* 1974. Growth and survival of haddock (*Melanogrammus aeglefinus*) larvae in relation to planktonic prey concentration. – J. Fish. Res. Bd. Can. 31: 1415-1419.

*Majkowski, J.* 1977. Prognosis for catches of cod, herring and sprat in the Baltic Sea, and their optimization with the aid of the mathematical model. – Pol. Arch. Hydrobiol. 24: 361-382.

*Mandecki, W.* 1976. A computer simulation model for interacting fish populations studies, applied to the Baltic. – Pol. Arch. Hydrobiol. 23: 281-307.

*Mills, C.A.* 1982. Factors affecting survival of dace, *Leuciscus leuciscus* (L.), in the early post-hatching. – J. Fish Biol. 20: 645-655.

*Thurow, F.R.* 1978. The fish resources of the Baltic Sea. – FAO Fish. Circ. No. *708.*

*Ursin, E.* 1967. A mathematical model of some aspects of fish growth, respiration and mortality. J. – Fish. Res. Bd. Can. *24:* 2355-2453.

*Ursin, E.* 1973. On the prey size preference of cod and dab. – Meddr Danm. Fisk- og Havunders. *7:* 85-98.

*Werner, R.G.,* (*Clupea harengus*) in relation to prey density. – Can. J. Fish. Res. Aquatic Sci. *37:* 1063-1069.

*Załachowski, W.* Feeding of cod in southern Baltic in 1977-1984. – *In* ICES Cooperative Research Report (in press).