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The effect of size-selective mortality on the size-at-age of Baltic herring

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Abstract

It is shown that the decrease in predation mortality by cod can explain the major part of the decrease in mean size-at-age which has been observed for herring stocks in the Baltic proper during the 1980s. The underlying quantification of the vital rates starts by assuming constant growth. From the von Bertalanffy Growth Equation (VBGE), Individually-Based Growth Models (IBGMs) are developed with the same mean VBGE. Three IBGMs that differ with respect to individual size at old age are considered. ICES Multispecies Virtual Population Analysis shows that the predation mortality on herring longer than 10 cm has decreased 30-fold but has maintained the same allometric relationship. This relationship states that mortality-at-size is inversely proportional to body-length to the power of ca. 5. Such a power is consistent with a size-preference by cod in which the optimal predator/prey size-ratio increases with increasing predator size. Computer simulations of lengths-at-age for the 1981-year-class of herring are compared with data from hydroacoustic surveys.

Keywords: Baltic herring, Individually-Based Growth Model (IBGM), size-specific predation, apparent growth.

1. Introduction

Growth of herring in the Baltic Sea has been investigated for many years (e.g. Popiel 1958). In the last decade the mean weight-at-age for herring has changed (Figure 2B, C). These changes have been related to variations in predation pressure (e.g. Sparholt & Jensen 1992), changes in relative recruitment strength between southern and northern stock components (e.g. Sjöstrand 1992) and to changes in hydrographical conditions, (e.g. Wyszynski 1988, 1991). However, no definite conclusion on the causal relationship has yet been reached (Sparholt 1994). The relevant question in fish stock assessment and yield prediction is whether the observed decrease in mean size-at-age during the 1980s is due to unpredictable phenomena or whether it can be explained by predictable changes in growth, predation, migration patterns etc. Sparholt (1991) drew attention to the simultaneous decrease in the stock of Baltic cod and the aim of this paper is to quantify the effect of the dynamics of predation on the size-at-age of herring.

The herring in the Baltic proper (ICES subdivisions 25-29; Figure 1) is a composite of herring populations with different growth characteristics (Voipio 1981). For example, a herring of 20 cm length can be from 1 to 10 years of age. Furthermore,

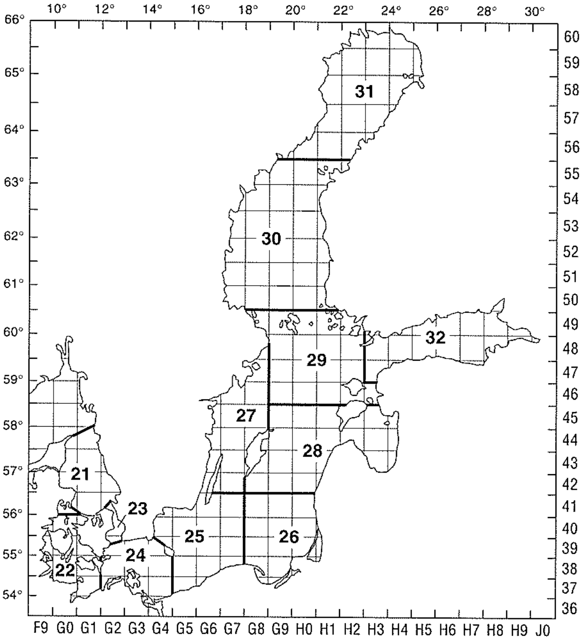


Figure 1. Map of the Baltic Sea showing the ICES subdivisions for stock assessment.

in any real situation the observed distributions of lengths-at-age have been influenced both by growth and by size-selective mortality (both fishing and natural) and migration. Therefore it is impossible to determine growth from the observed increments in lengths-at-age (referred to as 'apparent growth' in this study) without a quantitative evaluation of the size-specific effects of the other factors. The problem is ignored in traditional fish stock assessment by considering only mean length-at-age and not the underlying distributions of lengths-at-age and their causes. It is tacitly assumed (often incorrectly) that the observed increments in mean lengths reflect actual growth only. In this study the term 'growth' is used exclusively to designate somatic growth. The starting point is therefore that the apparent growth is not simple to relate to the actual growth. Restricting the samples to a small area makes influence of migration large, while integrating samples over a large area eliminates migration; but in that case herring with different growth rates are included in the analysis. In the present attempt of eliminating other factors than predation, the last approach is followed and subdivisions 25-29 considered to comprise one population of herring with constant growth characteristics for the individual fish during the 1980s. It is the variability in such individual characteristics that permits a quantification of herring populations with quite different growth rates. We furthermore eliminate possible effects of hydrographic changes on the size-at-age of small herring by considering only one year-class of herring. The basic components required for the development of a simulation model of the size-at-age of a population of herring are then reduced to quantifications of the variations in growth and mortality at size.

Three simple growth hypotheses are incorporated in this study. The first one is the traditional von Bertalanffy Growth Equation (VBGE) as applied in Figure 2.

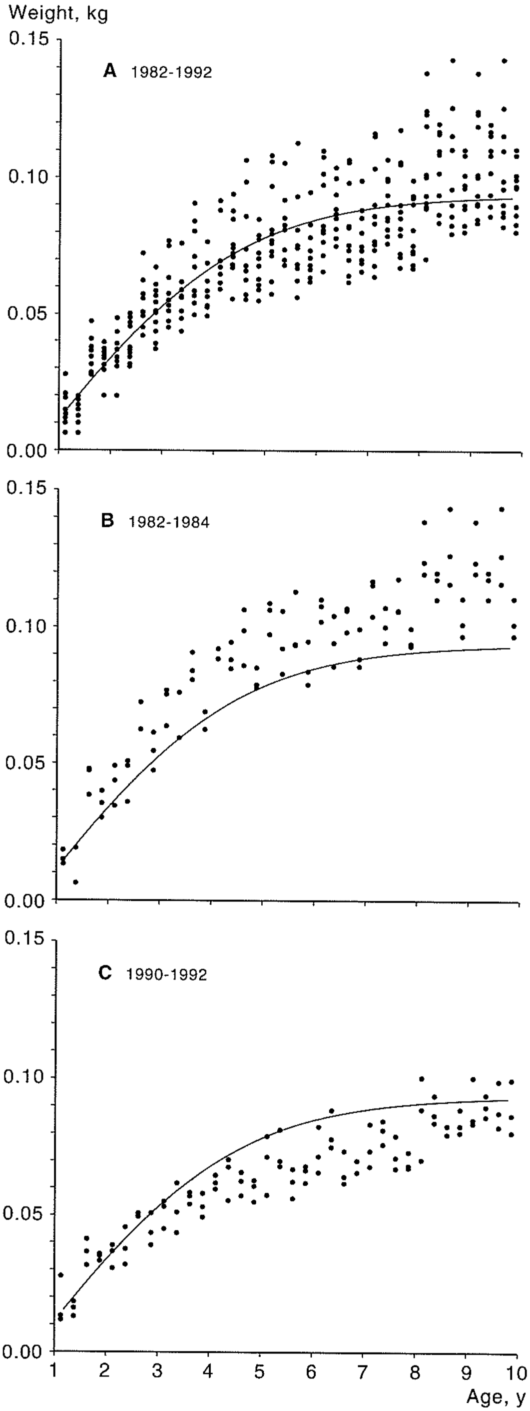


Figure 2. Mean weight-at-age for Baltic herring in ICES subdivisions 25-27 from Anon. (1994).
A: period 1982-92 with von Bertalanffy growth curve fit from non-linear estimation of the parameters in the model:
$\ln W = \ln \overline{W}_\infty + 3 \cdot \ln(1 - \exp(-K \cdot (t - t_0)))$:
$\hat{K} = 0.53\ \mathrm{y}^{-1}$ (s.e. = $0.03\ \mathrm{y}^{-1}$),
$\widehat{\ln \overline{W}_\infty} = -2.36$ (s.e. = 0.02) and
$t_0 = -0.30$ y (s.e. = 0.09 y);
B: mean weights at age for 1982-84 are above the estimated growth curve for the entire period 1982-92;
C: mean weights at age for 1990-92 are below the estimated growth curve for 1982-92.

The two others are also based on the same VBGE-mean-reference curve but assume that the standard deviation (s.d.) of length-at-age, respectively the coefficient of variation (c.v.) of length-at-age is constant as the cohort grows up (in the absence of size-selective mortality). We will show that these Individually-Based Growth Models (IBGMs) can be described by VBGE with the same curvature parameter (K) but with different asymptotic lengths at old age (L_∞). The IBGMs are presented in Section 3.1. The biological rationale for individually varying L_∞s is discussed in Section 5.1.

The ICES Multispecies Virtual Population Analysis (MSVPA) is used as a data source on mortality. The aim is to extract the key information on the size-specific mortalities from the vast MSVPA-output (Anon. 1994). The basic question asked is whether predation mortality bears a simple allometric relationship to the size of the herring. Previous attempts at this have explained only 20-40% of the mortality variation (e.g. Sparholt & Jensen 1992). As with the IBGMs, the quantification of size-specific mortality is first considered as a separate task. The models are presented in Section 3.2 and the parameters estimated in Section 4.1. By removing the (annual) effect of the reduction in the spawning stock biomass of cod it is shown that an allometric model can explain 94% of the variation in the predation mortalities. Using simple biomass size-spectrum theory the predator-prey ecology caused by this relationship is discussed in Section 5.2.

Thus the aim of this paper is first to introduce individual biological parameters in simple quantifications of size-specific growth and mortality. Secondly, using these individually-based models in the transfer to the population level, this paper describes a simulation model of the development in the distribution of lengths-at-age in a cohort. A simulation starts with the observed distribution of individual lengths in the cohort at some initial time. With the choice of IBGM and parameter values, the computer program delivers size-specific fishery and population statistics for each year-class on, for example, a quarterly basis. The relevant outcome in the present context is data on apparent growth (Section 4.2). As an example, the model is then applied to the 1981 year-class of Baltic herring. The results are compared with lengths-at-age obtained from hydroacoustic surveys (Section 4.3). The effect of mortality on the distribution of length-at-age of this year-class is discussed in Section 5.3. It is shown that the observed decrease in mean length-at-age of herring in the Baltic proper virtually can be explained by the decrease in the predation mortality by cod without assuming any changes in the conditions for growth during the 1980s.

2. Material and methods

The predation mortalities estimated by MSVPA (Anon. 1994) for herring, age groups 1-9, in subdivisions 25-27 in 1982-92 are used to derive the predation mortality by cod on a quarterly basis. Following MSVPA, the mean weights-at-age in the catch (cf. Figure 2) are considered representative for the mean weight-at-age in the population. These weight data are here considered as the independent variable of body-size in a simple analysis of size-specific mortality.

Only mortality- and possible migration-contaminated information on growth of herring was available for the present study. The case considered is based on length distributions-at-age from the international hydroacoustic surveys described in Anon. (1987). These surveys are conducted annually in late September and October and the surveys cover subdivisions 24-29, see Figure 1. Sjöstrand (1992) gives the resulting length distributions at age 0-10 for 1982, 1986 and 1990. These data present two major problems for the present purpose. First, it is not possible to infer apparent growth rate from one annual October picture of the stock composition unless steady state conditions are assumed which is not appropriate. Sjöstrand (pers. comm.) kindly provided the same type of data for 1983-85 so that the mortality dynamics could be considered and the possible effect of size-specific recruitment variations could be sorted out by following individual year-classes. The second problem relates to subdivision 24 which also comprises juveniles of the Rügen spawning herring. This stock component migrates down from the Skagerrak/North Sea to subdivision 24 and spawns somewhat earlier than the spring spawners east of Bornholm. The Rügen herring component is known to bias the growth picture for subdivisions 24-29. It will dominate the right-hand tail of the length distributions (i.e. relatively big fish) in particular for age group 0 and 1 whereas its contribution to the fully matured age groups is marginal. Sjöstrand (pers. comm.) provided the separate data for subdivision 24 for some years which made it possible to construct (incomplete) pictures of apparent growth for the early 1980s-year-classes in subdivisions 25-29. Age group 0 from the acoustic surveys was not considered representative for the population due to the inaccessibility of the coastal areas. In this study only the 1981 year-class is considered, and Table 1 (next page) shows the length distributions-at-age according to the data available. The mean length of the group-1 fish from subdivisions 24-29 in 1982 was 16.4 cm (cf. Sjöstrand 1992). Because the mean length of the fish in subdivision 24, contributing ca. 25% by numbers, was 18.0 cm, by removing the contribution from subdivision 24, the mean length is reduced to 16.0 cm (first column of Table 1). Age group 3 and 5 have similarly been adjusted although the contributions from subdivision 24 were marginal for these age groups. Data were not available for adjusting the other age groups.

Deterministic simulations of size-specific cohort dynamics are developed here for the purpose of dealing with length-at-age distributions, i.e. length-class based discrete approximations to continuous number densities over length. The computer program applied is a simple implementation of the principle that all fish of the same size belonging to the same cohort exhibit identical growth. In the program this is done by representing the initial cohort length distribution by the number of live fish in a series of class mid-points on the length axis and then for each time step transform these mid-points according to the growth transformation. Using a standard iterative Euler method, numbers are at the same time decreased according to the total size-specific cumulative mortality that each mid-point grows through in each transformation. The three IBGMs are based on VBGE which implies that the mid-point growth transformation in every case can be calculated exactly independent of the length of the time-step involved. It also implies equidistant mid-points at any point in time. For fitting purposes the variances are adjusted with the Sheppard's correction, (by subtracting the length of class interval squared divided by 12 from the grouped variance).

Table 1. Length-at-age of the 1981 herring year-class obtained from the international hydroacoustic surveys in October in the Baltic Sea, ICES subdivisions 25-29. The 1983 column (2-ringers) includes an unknown contribution from subdivision 24. The age groups 4 and 9 contain likewise a small but unknown contribution from subdivision 24. Contributions from subdivision 24 have been subtracted (from the original data available pertaining to ICES subdivisions 24-29) for the other age groups. The negative numbers which result for two length groups in 1982 are set to zero in the analysis.

L_{lower}, cm	1982 Age 1	1983 Age 2	1984 Age 3	1985 Age 4	1986 Age 5	1990 Age 9
32					1	
31						
				1		1
30						1
					2	
29				2	1	4
			1	3		6
28			1	5	5	11
		1	2	12	6	10
27			9	15	12	19
			9	27	12	20
26		4	29	26	25	26
		8	37	32	34	17
25		13	48	40	35	19
		32	76	61	39	5
24		30	80	67	74	2
		71	96	78	75	30
23		84	76	93	117	12
		112	108	128	145	1
22		115	109	189	156	2
		165	155	192	151	5
21	8	161	183	214	212	
	(- 13)	176	200	258	198	3
20	(- 8)	189	305	265	244	
	24	201	365	253	178	
19	113	254	473	264	240	
	217	295	456	202	179	
18	276	358	441	171	183	
	254	406	389	143	137	
17	231	401	400	100	76	
	484	338	301	97	34	
16	487	364	265	59	28	
	444	382	234	15	12	
15	537	364	121	18	3	
	503	203	48	3	1	
14	421	95	14	4		
	249	30	12	1		
13	74	11				
	12					
12	5					
N	4339	4863	5043	3038	2615	194
$\bar{L}$	16.05	18.20	19.14	20.56	20.73	25.74
s.d.	1.566	2.549	2.525	2.485	2.364	1.937
c.v.	0.0976	0.1400	0.1319	0.1209	0.1140	0.0752

3. Modelling growth and mortalities

3.1. *Growth*

In the absence of size-selective mortality the mean length-at-age is assumed to be described by a certain Reference Mean Growth Curve independent of the variability in growth among the individuals of the year-class (cohort) considered. The task of the IBGMs described below is to account for the spread-out of individual lengths around this mean growth curve. Focus is placed on normally distributed lengths-at-age. In the Contractive Growth Model the distribution continues to tail-off more and more rapidly. This narrowing down is in contrast to the expansion which takes place in the Constant C.V. Growth Model. The Equal Variance Growth Model (Constant S.D. Growth Model) is in between. In each case the individual length-increments are calculated in an exact procedure by the computer. Figure 3 illustrates the principle and Figure 4 (next page) gives an example of the result.

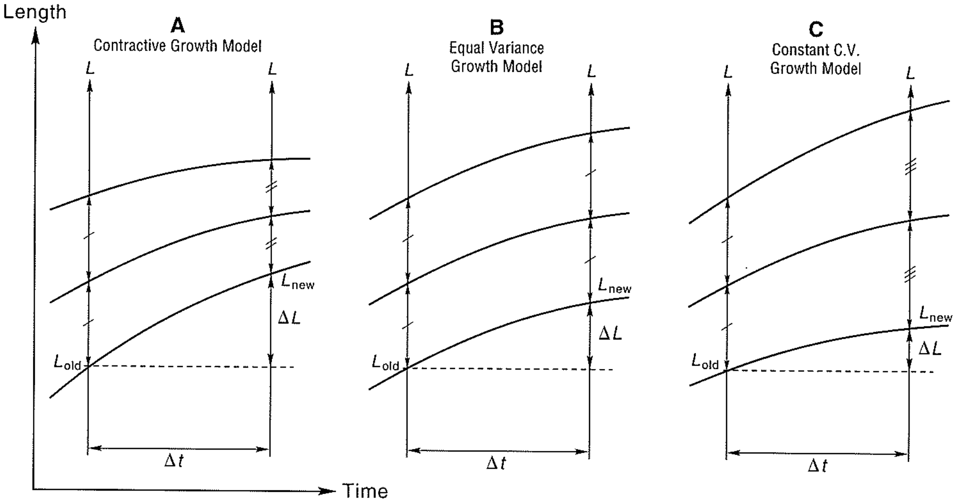


Figure 3. Individually-based growth trajectories during a time step. A: the growth increment, ΔL, decreases with increasing length of the fish (L_{old}) in the Contractive Growth Model; B: remains constant in the Equal Variance Growth Model (Constant S.D. Growth Model); and C: increases in direct proportion to L_{old} in the Constant C.V. Growth Model.

3.1.1. *Reference Mean Growth Curve*

The reference mean growth curve, $\bar{L}_r(t)$, is determined by VBGE$(K, \bar{L}_{r\infty})$, i.e. $d\bar{L}_r/dt = K(\bar{L}_{r\infty} - \bar{L}_r)$ and, hence

$$\bar{L}_r = \bar{L}_{r\infty} - [\bar{L}_{r\infty} - \bar{L}_{r0}] \exp(-Kt) \tag{1}$$

where time zero refers to the real time at which the initial distribution of lengths-at-age was collected (e.g. the normal distribution at age-1-year in Figure 4). Unless otherwise specified $\bar{L}_{r0}$ denotes the mean length of this initial distribution. It is with the purpose of keeping a simple notation that time zero (index 0) is used in Section 3.1 to designate the initial condition. In any real situation (Sections 4 & 5) it is more

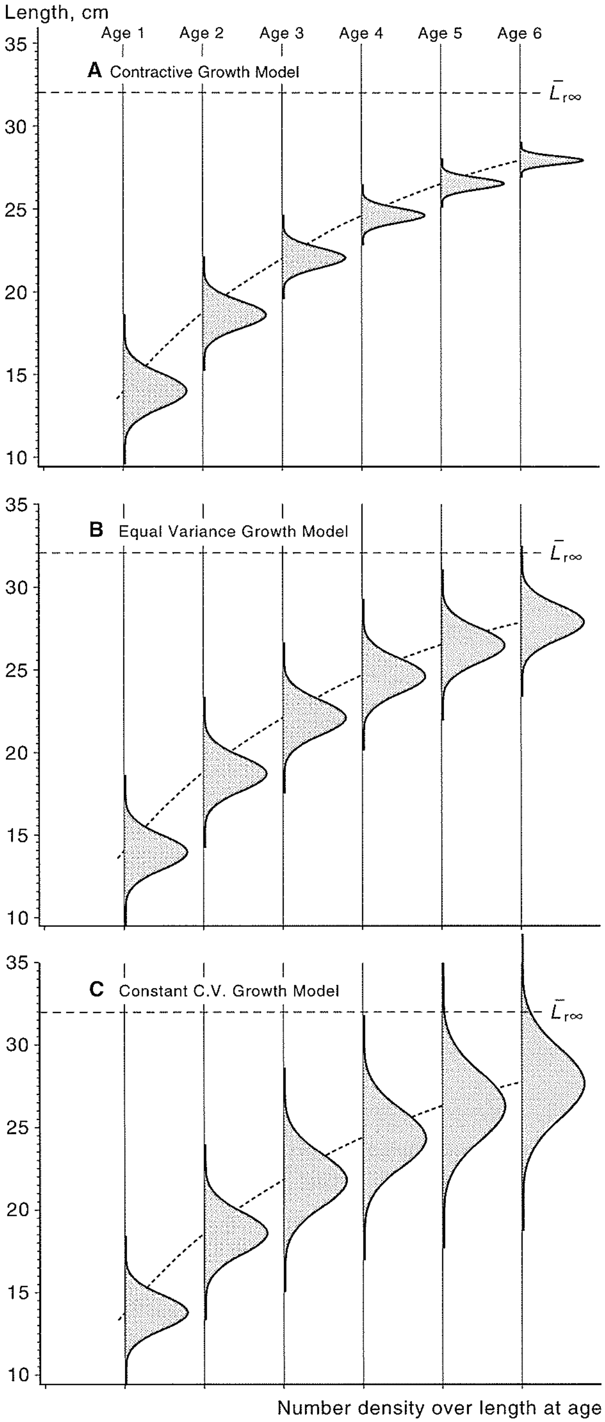


Figure 4. An example of cohort growth according to the three IBGMs in the absence of size-selective mortality. The number densities over lengths-at-age have all been normalized to the same maximum value. Initially, at age 1, the fish in the cohort are normally distributed with mean 14 cm and standard deviation 1 cm, i.e. c.v. = 1/14. They all grow with $K = 0.3$ y^{-1}. The Reference Mean Growth Curve is VBGE (0.3 y^{-1}, 32 cm). This $\bar{L}_{r\infty}$ of 32 cm is also shown. The mean length at age 6 becomes 28.0 cm.
A: the standard deviation (s.d.) is diminishing exponentially. After 5 years at age 6, s.d. is reduced by almost a factor of 5 to exp(−1.5) = 0.22. No fish will grow beyond $\bar{L}_{r\infty} = 32$ cm. Note that with mortality equal to zero and if the max-densities had not been normalized, the normal peak should increase to account for the initial number of fish as the distribution continues to narrow down.
B: s.d. is maintained. A small fraction of the fish are larger than $\bar{L}_{r\infty}$ at age 6, i.e. the tail from mean plus four s.d. Half of the live fish at old age will be larger than $\bar{L}_{r\infty}$.
C: s.d. increases in direct proportion to mean length. At age 6 when the mean length has increased by a factor of 28/14 = 2, s.d. has likewise doubled. Thus, the largest ca. 2.5% of the fish has already grown beyond $\bar{L}_{r\infty}$ at age 6. Note that with mortality equal to zero (and if the max-densities had not been normalized), the peak should decrease to account for the initial number of fish as the distribution continues to spread out.

convenient to relate initial conditions to true age (e.g. $\bar{L}_{r1}$ refers to the reference mean length at age 1) or to real time (e.g. $\bar{L}_{r1982}$). Possible abuse of the formulae in Section 3.1 should be avoided by interpreting t as a Δt, i.e. the time since the initial events took place.

3.1.2. *Contractive Growth Model*

All members of the cohort follow the same VBGE (K, $\bar{L}_{r\infty}$). Fish with initial length L_0 attain length L at time t with the growth rate,

$$\mathrm{d}L/\mathrm{d}t = K(\bar{L}_{r\infty} - L) \tag{2}$$

Hence, using Eq. 1 in a modified form,

$$L = L_0 \exp(-Kt) + \bar{L}_{r\infty}(1 - \exp(-Kt)) \tag{3}$$

It is of note that at any fixed time L is linear in L_0. If L_0 is normally distributed with mean $\bar{L}_{r0}$ and standard deviation σ then L will be distributed with mean $\bar{L}_r$ as given by Eq. 1 and standard deviation,

$$\text{s.d.} = \sigma \exp(-Kt) \tag{4}$$

Thus the distribution continues to be normal as time evolves with a standard deviation that is reduced at an exponential rate. Note that σ is not necessary small even if time zero refers to age zero. In accordance with standard assessment procedure, the cohort is considered to comprise fish of the same age although the actual individual ages may vary considerably due to an extended spawning season. This among other things accounts for the initial s.d.-at-age in the applications of the model to Baltic herring.

3.1.3. *Equal Variance Growth Model*

All members of the cohort grow exactly at the same rate. Using VBGE, this implies firstly that all members are growing with the same curvature parameter, K. Secondly, by requiring that the initial growth rate for fish of size L_0 (growing towards L_∞) equals the growth rate for a fish of size $\bar{L}_{r0}$ (growing towards $\bar{L}_{r\infty}$), we obtain

$$L_\infty - L_0 = \bar{L}_{r\infty} - \bar{L}_{r0} \tag{5}$$

The initial size difference, $L_0 - \bar{L}_{r0}$, is maintained throughout life (in the absence of size-selective mortality). Thus the growth curve for a fish of size L_0 at time 0 is determined by VBGE(K, $\bar{L}_{r\infty} + L_0 - \bar{L}_{r0}$), that is

$$\mathrm{d}L/\mathrm{d}t = K(\bar{L}_{r\infty} + L_0 - \bar{L}_{r0} - L) \tag{6}$$

and, hence

$$L = L_0 + (\bar{L}_{r\infty} - \bar{L}_{r0})\,(1 - \exp(-Kt)) \tag{7}$$

The shape of the initial distribution of lengths-at-age and its s.d. remain constant and mean growth is again described by Eq. 1. It may be noted that Eq. 5 also is obtained as a (mathematical) consequence of the requirement of maintaining a normal distribution and its s.d. of lengths-at-age.

The difference between this model and the contractive model is simply that the growth curve for an individual fish in the contractive model is obtained by displacing the Reference Mean Growth Curve (RMGC) parallel to the time axis whereas the RMGC-displacement here takes place parallel to the length axis.

3.1.4. *Constant Coefficient of Variation Growth Model*

This model of constant c.v. is based on the normal distribution *or* the log-normal distribution for lengths-at-age and still using VBGE at the individual level. We state without proof that the requirement of maintaining the shape of the distribution and its c.v. in both cases lead to

$$L = \frac{L_0}{\bar{L}_{r0}} \bar{L}_r = L_0 \left[\bar{L}_{r\infty}/\bar{L}_{r0} - (\bar{L}_{r\infty}/\bar{L}_{r0} - 1) \exp(-Kt)\right] \tag{8}$$

In the reverse argument, Eq. 8 shows that if L_0 is normally distributed then so is L and the c.v. remains constant because the standard deviation increases in direct proportion to the mean, i.e.

$$\text{s.d.} = \sigma \left[\bar{L}_{r\infty}/\bar{L}_{r0} - (\bar{L}_{r\infty}/\bar{L}_{r0} - 1) \exp(-Kt)\right] \tag{9}$$

If instead $\ln(L_0)$ is normally distributed with variance β^2 then so is $\ln(L) = \ln(L_0) + \ln(\bar{L}_r/\bar{L}_{r0})$. Thus the c.v. $= [\exp(\beta^2) - 1]^{1/2}$ of log-normally distributed lengths-at-age is fixed because of Eq. 8.

The growth curve for fish of size L_0 at time 0 is determined by VBGE $(K, \bar{L}_{r\infty} L_0/\bar{L}_{r0})$. It also follows directly from Eq. 8 that

$$\frac{1}{L}\frac{dL}{dt} = \frac{1}{\bar{L}_r}\frac{d\bar{L}_r}{dt} \tag{10}$$

so in this model all members of the cohort grow at exactly the same *specific* growth rate determined by Reference Mean Growth. The initial ratio of length to mean length, $L_0/\bar{L}_{r0}$, is maintained throughout life (in the absence of size-selective mortality).

3.2. *Mortalities*

In accordance with MSVPA, Z, the total rate of instantaneous mortality, is composed of the fishing mortality (F), the predation mortality ($M2$) and an unknown residual natural mortality ($M1$), i.e. in size-specific terms

$$Z(L,t) = F(L,t) + M2(L,t) + M1 \tag{11}$$

The aim is to describe the mortality dependency on length through simple size-specific models of fishing and predation. Adding a constant such as M1 or a function of time only is not going to affect apparent growth because it will decrease numbers-at-length during a time-step by the same factor independent of length.

3.2.1. *Fishing mortality*

The fishing mortality depends on the size of the fish through both selection and availability on the fishing ground since migration is often size dependent. Retention in a trawl fishery is usually quantified by the S-shaped logistic curve (e.g. Sparre & Venema 1992),

$$S(L) = 1/(1 + \exp(-r(L - L_{50}))); \; r = 2 \ln 3/S.R. \; ; \quad L_{50} = S.F. \cdot \text{Mesh Size} \tag{12}$$

where L_{50} denotes the length at 50% retention, *S.F.* the selection factor and *S.R.* the selection range. Let the selection pattern i.e. the fishing mortality dependence on size be $S(L)$ and let the annual and seasonal variation be accounted for by variation in effective effort E(year, season) then

$$F(\text{year, season}, L) = c\,E(\text{year, season})\; S(L) \tag{13}$$

where c is the catchability coefficient.

3.2.2. *Predation Mortality*

Multispecies models operate with predation as a key element in describing the natural mortality. This predation is dependent on the predator biomass, B_{predator}, and the prey biomass, B_{prey}. The link between these two biomasses reflects the need for food by the predator. This need is temperature dependent and therefore a seasonal variation is introduced. As large fish eat small fish and, in the Baltic, nothing eats large fish, the predation mortality decreases as prey size increases. This is modelled by

$$M2(\text{year, season}, L) = P(\text{year})\; M2_{\infty}(\text{season})\; [L_{\infty}/L]^{p} \tag{14}$$

where the power, p, is expected to be equal to or greater than one. L_{∞} is here used only as a reference length. To account for seasonality in the predation pressure the maximum predation mortality for large prey ($L = L_{\infty}$), $M2_{\infty}$, is made dependent on season. Migration may add to the complexity of the system by altering the predator/prey biomass ratio over the year the effect of which also is assumed accounted for by the seasonal dependency of $M2_{\infty}$. P is a relative (dimensionless) scaling-factor that accounts for annual variations in the relevant predator / prey biomass ratio during the entire period of time considered.

4. **Results**

In the present study simple isometric growth is assumed, i.e. the length to weight relationship for Baltic herring becomes

$$W = q \cdot L^{3} \; ; \qquad q = 0.006 \text{ g} \cdot \text{cm}^{-3} \tag{15}$$

where the estimate of q, the condition factor (divided by 100) is obtained as a subdivision average from a recent unpublished study based on Swedish weight-at-length data for 1992 (K.J. Stæhr, pers. comm.).

4.1. *Parameter estimation: mortalities*

The fishing mortality is small and the effort has remained relative stable over the entire period (Anon. 1994). Thus, neglecting annual and seasonal variations, the parameters of $F(L)$ were simply obtained by eye-fitting an average trawl-selection curve to the F-at-age outcome of the MSVPA using the length-weight relationship in Eq. 15 and, at the same time taking knowledge of the commercial gear into account. The result is

$$F(L_{[\mathrm{cm}]}) = 0.25/(1 + \exp(-0.55(L - 12.8)))\ \mathrm{y}^{-1}$$

corresponding to a selection factor and range of 4, *S.F.* = *S.R.* = 4, and a mesh size of 32 mm. Hence, the maximum fishing mortality is $F_{\max} = cE = 0.25\ \mathrm{y}^{-1}$, half of which is reached at $L_{50} = 12.8$ cm.

The natural mortality of other causes than predation, i.e. the residual mortality $M1$, is considered constant at $0.2\ \mathrm{y}^{-1}$ in accordance with MSVPA.

The parameters of predation mortality were estimated by linking the mean body weights in the catch (see Figure 2A) to the predation mortalities by age, year and quarter as obtained from MSVPA (Anon. 1994). First by neglecting the possible effect of annual and seasonal variations and by utilizing the assumption of isometric growth, the predation model in Eq. 14 was reduced to

$$M2 = M2_{\infty}(L_{\infty}/L)^{p} = M2_{\infty}(W_{\infty}/W)^{p/3} \tag{16}$$

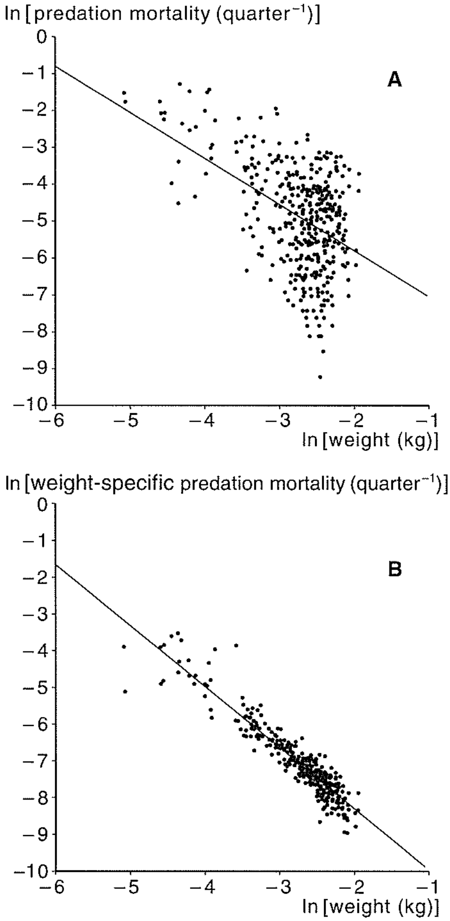


Figure 5. Double logarithmic plots of MSVPA-predation mortalities per quarter on Baltic herring in subdivisions 25-27 against mean body weights for age groups 1-9 in the period 1982-92. A: the slope of the fitted line is −1.25 (s.e. = 0.12); $r^2 = 0.22$;
B: exactly the same paired data, $(x_i, y_i) = (\ln W_i, \ln M2_i)$; $i = 1,2,..,396$, as in ‘A’ but the estimated annual and seasonal effects have been subtracted from $\ln M2$, i.e. the y-value of each of the 9 points in ‘A’ that refers to a specific quarter in a specific year is reduced by the same amount, YEAR + QUARTER, given in Table 2. The slope of the fitted line is − 1.722 (s.e. = 0.035); $r^2 = 0.94$.

Figure 5A gives a double logarithmic plot of $M2$ [quarter^{-1}] against W[kg]. The estimated line with $p = 3.74$ (s.e. = 0.35), i.e. the allometric model in Eq. 16, explains 22% of the variance. The analysis was extended to

$$\ln(M2) = \text{CONSTANT} + \text{YEAR} + \text{QUARTER} - p/3 \cdot \ln(W) \qquad (17)$$

with the result that both the annual term (YEAR), the seasonal term (QUARTER) and the regression term ($p/3 \cdot \ln W$) all significantly contributed to the description of the variation in the predation mortalities. The parameter estimates are given in Table 2. Subtracting the estimated effect of annual and seasonal variations, Figure 5B shows the resulting plot of residual log-size-specific-mortality against log-body-weight. The estimated allometric model in Eq. 17 with $p = 5.165$ (s.e. = 0.1) explains 94% of the variance. Transforming Eq. 17 to the notation in Eq. 14 using again the length-weight relationship in Eq. 15 yields with $L_\infty = 25$ cm as reference

$$M2(\text{year, quarter}, L_{[\text{cm}]}) = P(\text{year}) \cdot M2_\infty(\text{quarter}) \cdot [25/L]^{5.165} \ \text{y}^{-1} \qquad (18)$$

where the factors P(year) and $M2_\infty$(quarter) are given in Table 2. Thus the size-specific form of the predation mortality is invariant over time but the level of predation

Table 2. Specification of the model of size-specific predation on herring by cod in the Baltic Sea, ICES subdivisions 25-27 in 1982-92. Mortality is expressed relative to 1982 (i.e. $P(1982) \equiv 1$) and $L_\infty = 25$ cm and the model reads $M2$(year, quarter, $L_{[\text{cm}]}$) y^{-1} equals P(year) · $M2_\infty$(quarter) · $(25/L)^{5.165}$. The annual (dimensionless) factor P(year) and the seasonal factor $M2_\infty$(quarter) in units of y^{-1} are derived from ANOVA estimates of the parameters in the additive model $\ln(M2_{[\text{per quarter}]})$ = INTERCEPT + YEAR + QUARTER + SLOPE · $\ln(W_{[\text{kg}]})$. INTERCEPT is estimated to − 11.6655 (s.e. = 0.1184) with reference to YEAR = 0 and QUARTER = 0 for 1992 and the 4th quarter (Q4), respectively. SLOPE is estimated to −1.7216 (s.e. = 0.03479) and $r^2 = 0.938$. The number of observations in the data set is 396.

Year	P(year), dim. less.	ANOVA YEAR	s.e.
1982	1	3.4008	0.0829
1983	0.901	3.2971	0.0828
1984	0.802	3.1799	0.0826
1985	0.531	2.7683	0.0821
1986	0.414	2.5182	0.0822
1987	0.268	2.0839	0.0821
1988	0.291	2.1655	0.0823
1989	0.186	1.7185	0.0822
1990	0.104	1.1343	0.0821
1991	0.0556	0.5111	0.0821
1992	0.0333	0	

Quarter	$M2_\infty$(quarter), y^{-1}	ANOVA QUARTER	s.e.
1st quarter	0.0332	− 0.6013	0.0496
2nd quarter	0.0539	− 0.1173	0.0495
3rd quarter	0.1374	0.8182	0.0496
4th quarter	0.0606	0	

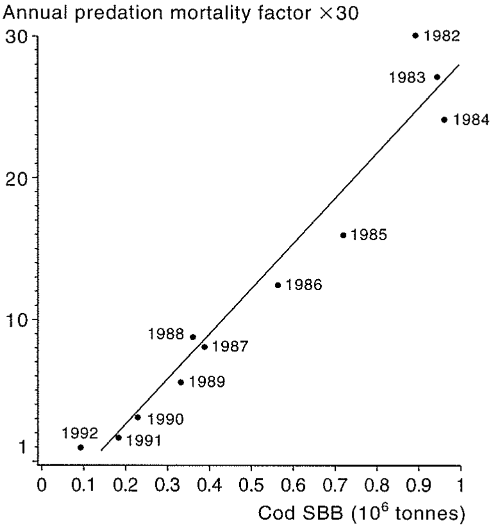


Figure 6. Plot of estimated annual predation factor, P(year) (normalized to a minimum value of one), against the cod Spawning Stock Biomass (SSB). The reduction in cod SSB can explain that the level of size-specific predation on Baltic herring by cod in ICES subdivisions 25-27 has decreased 30-fold from 1982 to 1992.

has decreased with a factor of 30 from 1982 to 1992. This decrease can be related to the simultaneous decrease in the spawning stock biomass of cod, see Figure 6A. Adding the three components of mortality yields total mortality

$$Z(\text{year, quarter}, L_{[\text{cm}]}) = M1 + M2(\text{year, quarter}, L_{[\text{cm}]}) + F(L).$$

As an example, Figure 7 depicts the seasonal averaged length-specific mortality situation in 1982 and in 1992. The average of $M2_\infty$(season) over a calendar year becomes $\overline{M2}_\infty = 0.0713\ \text{y}^{-1}$ and hence the predation mortality component shown in Figure 7,

$$M2(\text{year}, L_{[\text{cm}]}) = P(\text{year}) \cdot 0.0713 \cdot (25/L)^{5.165}\ \text{y}^{-1} \tag{19}$$

where $P(1982) = 1$ and $P(1992) = 1/30$. Thus the average predation mortality depicted in Figure 7 corresponds roughly to the situation in the 4th quarter since $M2_\infty(\text{Q4}) \approx \overline{M2}_\infty$ according to Table 2. Approximately half this level operates in the 1st quarter whereas double the level gives the situation in the 3rd quarter.

4.2. *Principal effects of size-selective predation: apparent growth*

The growth situation shown in Figure 4 is used here as a basis for gaining insigt into the general effect of cod predation on the length-at-age of herring in the sea. Thus lengths at age 1 year are considered normally distributed with mean 14 cm. If the rate of mortality was constant for all sizes of herring the mean length in the cohort would follow the VBGE (0.3 y^{-1}, 32 cm) curve (see Figure 4) and hence reach length 28.0 cm at age 6 irrespectively of the initial variance in size and the choice of growth model. It is necessary to determine how much the mean length at age 6 increases if the cohort has been exposed to a sustained predation mortality for five years that is described by the estimated 1982-level. Similarly for the 1992-situation. Also it is necessary to consider the effect of the initial variability in individual lengths on the

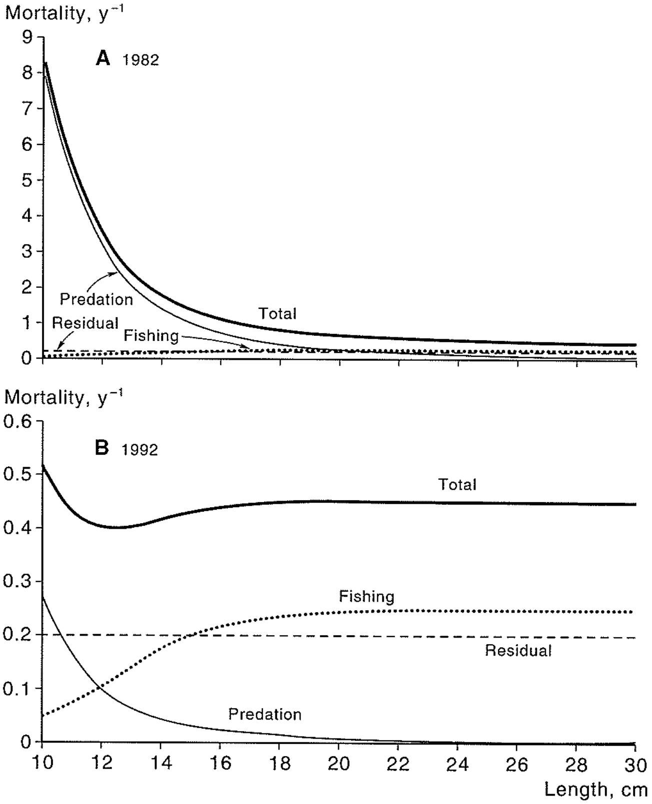


Figure 7. Total length-specific mortality averaged over seasons, $Z(\text{year}, L)$ (heavy solid line), for Baltic herring in subdivisions 25-27 in A: 1982; and B: 1992. Both the residual natural mortality (dashed), $M1 = 0.2\ \text{y}^{-1}$, and the fishing mortality, $F(L)$, the punctured logistic curve ($F_{\text{max}} = 0.25\ \text{y}^{-1}$, $L_{50} = 12.8$ cm and $r = 0.55\ \text{cm}^{-1}$), are considered to remain constant during 1982-92. The predation mortality, $M2$, decreases with increasing L as $L^{-5.165}$ but the annual level drops by a factor of 30 from 1982 to 1992. Adding the three components yields total mortality, $Z(\text{year}, L) = M1 + M2(\text{year}, L) + F(L)$.

development of the mean length in the cohort. In this context we also consider the question on how an observed (apparent) mean growth curve can be explained in terms of VBGE-parameters. Finally it is necessary to determine how an initial difference between the actual mean length in the cohort, L_1, and the Reference Mean Length, L_{r1}, resulting from e.g. the accumulated effect of size-selective predation during the first year of life (i.e. prior to the initial condition considered) will affect the growth curve for mean length-at-age.

We first consider the implications of the situation in the early 1990s, i.e. according to Eq. 19 the consequences of the size-specific mortality

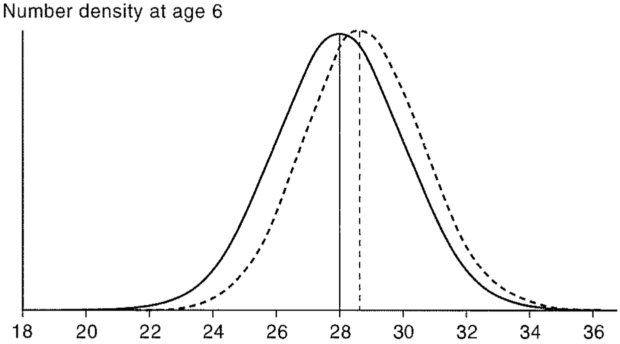
$$M2_{1992}(L_{[\text{cm}]}) = 0.000664 \cdot (32/L)^{5.165} \quad \text{y}^{-1}$$

The effect of this small mortality (see Figure 7B) on apparent growth is negligible (not shown). In the case of an initial s.d. of one as in Figure 4 the mean length at age 6 increases by 0.3 mm (0.1%) with the Constant C.V. Growth Model. As expected the effect is even smaller with the two other growth models.

The situation in the late 1970s and early 1980s is characterized by a 30-fold larger predation mortality (see Figure 7A),

$$M2_{1982}(L_{[\text{cm}]}) = 0.0199 \cdot (32/L)^{5.165} \quad \text{y}^{-1}$$

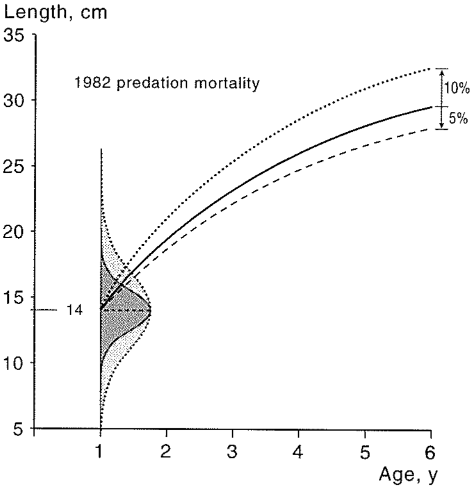
Figure 8. Simulated length distributions at age 6 with the Constant C.V. Model starting with N(14 cm, 1 cm^2) at age 1. The heavy curve is the Normal distribution, N(28, 2^2), in case of constant mortality-at-size and with mean growth according to VBGE(0.3 y^{-1}, 32 cm), i.e. the distribution that is depicted in Figure 4C. The dashed curve (which is *not* normal) has been scaled for comparison and shows how the distribution under the same growth conditions changes when the cohort instead has been exposed to the 1982-predation mortality during the 5 years.



The increase in mean length-at-age is also ca. 30 times greater than for the situation one decade later because the deviations of $L^{-5.165}$ from a linear relationship in L are small (being less than 5% in the 13-15 cm length range) when the (initial) variance of lengths-at-age is small. The mean length at age 6 increases by 0.2%, 1% and 3% in the three cases shown in Figure 4. Figure 8 shows the shift in the length distribution at age 6 in the Constant C.V. Model. The normal shape of the initial distribution is no longer maintained due to the non-linear (decreasing) size-specific mortality although the effect is small in the present case as explained above. The standard deviation is reduced compared to the non-size-selective situation for the same reason. The s.d.-reduction at age 6 is 3.5, 5 and 7.5% (Figure 8) in the three cases. Interest is now focused on the Constant C.V. Growth Model where the largest effect of size-selective predation takes place due to the diversion of the individual growth trajectories.

Figure 9 shows mean length-at-age in the Constant C.V. Growth Model with the 1982-level of predation mortality for increasing initial s.d. The bottom curve represents the mean growth curve in Figure 4C because mortality has no effect on size when all the members of the cohort are identical. The two other curves in Figure 9 will therefore approach this reference (bottom) curve if predation gradually shifts towards a non-selective situation such as the 1992-level. The situation changes considerably when the cohort experiences the maximum level of size-selective predation as shown in Figure 9. Doubling initial s.d. results in a ca. 3-fold increase in the mortality effect on mean length-at-age.

Each of the curves in Figure 9 may be considered as representing observed mean size-at-age for the cohort. Such empirical curves are traditionally explained by the VBGE-parameters, $\hat{K}$ and $\hat{L}_\infty$, obtained from Chapman plots (e.g. Sparre & Venema 1992), i.e. the linear regression of the annual mean length increment, $\Delta\bar{L}$, on the mean length at the beginning of the year. Correct estimates of the growth parameters ($K = 0.300\ y^{-1}$ and $\bar{L}_\infty = 32.0$ cm) are only obtained for the reference curve (Figure 9, bottom curve) as the mean growth increments here pertain exactly to VBGE. The effect of size-selective predation is an (apparent) increase in both of the VBGE-parameters. For example, the estimates $\hat{K} = 0.377\ y^{-1}$ and $\hat{\bar{L}}_\infty = 35.7$ cm are obtained from the five annual L-increments determined by the (top) curve in Figure 9 representing the situation of an initial standard deviation equal to 3 cm (s.d.$_1$ = 3 cm). The effect of size-selective mortality is greatest during the first year of simulation when the fish still are relatively small (hence, the apparent increase in K) which also is reflected by a considerable initial drop in c.v. (e.g. 31% in the case of s.d.$_1$ = 3 cm). The s.d.-at-age does continue to increase (e.g. 50% over 5 years when s.d.$_1$



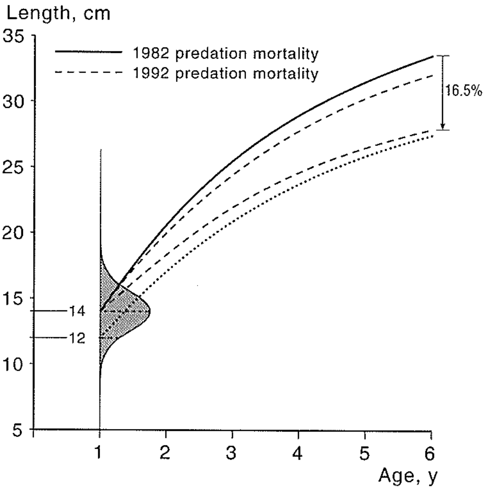


Figure 9. (left.) Example of the effect on growth curves for mean length-at-age of initial variations in the individual lengths. Growth and mortality are governed by the Constant C.V. Growth Model and the 1982-predation situation, respectively. Lengths at age 1 are normally distributed with mean 14 cm. The Reference Mean Growth follows VBGE(0.3 y^{-1}, 32 cm) as in Figure 4 and becomes identical to the bottom curve (dashed) for s.d. = 0. The top curve (punctured) refers to an initial s.d. of 3 cm (punctured, lightly shaded distribution) and the curve in between is obtained with half this standard deviation (solid, shaded distribution). Thus, using this curve for s.d.$_1$ = 1.5 cm as reference, the mean length at age 6 increases by 10% when s.d.$_1$ is doubled, and decreases by ca. 5% when s.d.$_1$ is reduced to 0 or when size-selective mortality ceases.

Figure 10. (right.) Example of the effect on growth curves for mean length-at-age of an initial difference between the actual mean length in the cohort ($\bar{L}_1$) and the reference mean length ($\bar{L}_{r1}$). Initial lengths at age 1 are normally distributed with mean 14 cm and standard deviation 1.5 cm. Growth is governed by the Constant C.V. Model with VBGE(0.3 y^{-1}, 32 cm) as reference mean curve. The dashed curves give mean length-at-age in the 1992 predation situation. The lower (dashed) curve is obtained when the reference mean length initially coincides with the mean length in the cohort ($\bar{L}_{r1} = \bar{L}_1 = 14$ cm). The reference mean growth curve (as depicted in Figure 4C) would on the graph be indistinguishable from the dashed curve, i.e. negligible effect (being 0.8 mm after five years) of the 1992-predation level. The upper (dashed) curve is obtained when the initial reference mean length has been reduced to $\bar{L}_{r1} = 12$ cm. The new Reference Mean Growth Curve is the punctured curve. The top curve shows the additional effect of a sustainable 1982-predation level (with $\bar{L}_{r1} = 12$ cm). The total effect of removing the 1982-level of size-selective predation is in this scenario a reduction by 16.5% in the mean length at age 6 years.

= 3 cm) but not as much as the increase in $\bar{L}$-at-age (e.g. 132% over 5 years when s.d.$_1$ = 3 cm). The percentage decrease in c.v. over the five years is doubled (from 18% to 36%) when s.d.$_1$ doubles from 1.5 to 3 cm.

This example can be developed where size-selective mortality during the first year of life increases the mean length at age 1 year by for example 2 cm. The (initial) reference mean length is reduced by 2 cm compared to the observed mean length at age 1, i.e. $\bar{L}_{r1}$ = 12 cm and $\bar{L}_1$ = 14 cm (Figure 10). The effect on growth in the Constant C.V. Model is equivalent to maintaining $\bar{L}_{r1} = \bar{L}_1$ = 14 cm but instead increasing $\bar{L}_{r\infty}$ by a factor of 14/12 or 17%. Thus a decrease in $\bar{L}_{r1}$ implies that the mean length-at-age in case of constant mortality-at-size increases with $\bar{L}_{r\infty}(\bar{L}_1/\bar{L}_{r1} - 1)[1 - \exp(-K\Delta t)]$ (cf. last term in $\bar{L}_r$-equation expressed on the form of Eq. 3) which in the present case becomes $32(2/12)[1 - \exp(-1.5)] = 4.14$ cm at age 6 years. The difference between the dashed curves (for the 1992 predation level) in Figure 10 is 32.20-28.06 = 4.14 cm. In this situation of $\bar{L}_{r1}$ = 12 cm the effect of introducing the 1982-predation level is a further 4.3%-increase in the (observed) mean length at age 6 ($\bar{L}_6$ = 33.59 cm). However, the relevant comparison must take into consideration that the effect of size-selective mortality in the 1990s also is expected to be negligible during the first year of life, i.e. $\bar{L}_1 - \bar{L}_{r1} = 0$ in 1992. If the difference $\bar{L}_1 - \bar{L}_{r1}$ actually has decreased by 2 cm during the early 1980s, the total effect of size-selective mortality during the first 6 years of life is then a decrease in mean length by 5.5 cm or 16.5% as shown on Figure 10.

4.3. *Case: 1981 year-class of herring*

All the data in Table 1 were utilized by applying standard non-linear techniques to VBGE on the form $\ln L = \ln \bar{L}_\infty + \ln(1 - \exp(-K \cdot (t - t_0)))$. The estimates become $\hat{K}$ = 0.209 y^{-1} (s.e. = 0.012 y^{-1}), $\ln \hat{\bar{L}}_{\infty[\mathrm{cm}]}$ = 3.215 (s.e. = 0.014) and $\hat{t}_0$ = −3.238 y (s.e. = 0.177 y). The length distribution for age 1 in 1982 was here associated with t_1 = 1.75 y which gives a calculated length of 16.1 cm using the estimates above. This length is equal to the mean length at age 1 in Table 1 (i.e. 16.05 cm) and K = 0.20 y^{-1} and $\bar{L}_\infty$ = 25 cm were consequently adopted as the only available VBGE-description of apparent mean-growth of the 1981 year-class from October 1982 onwards with the notation that $\bar{L}_\infty$ = 25 cm appears to be an underestimate. A simple trial and error procedure was then used to obtain approximative estimates of the parameters in the Constant C.V. Growth Model using lengths-at-age in 1982 (Table 1, column 1) as the start distribution. Mean Reference Growth of the 1981 year-class was considered described by K = 0.17 y^{-1}, $\bar{L}_{r\infty}$ = 25 cm and $\bar{L}_{r\,1982}$ = 15.25 cm.

Size-selective fishing mortality was included in all simulations and described by the estimated average-trawl-selection curve (independent of year and quarter). Size-selective predation was described by Eq. 18. However, the first quarter is Q4 since the simulations start on 1 October. The values of $M2_\infty$(season) for the three other quarters were reduced by a factor of 0.9 to account for the lower predation level in the next calendar year. This value represents the average annual-decay-factor in P(year) for the early 1980s where (for the 1981 year-class) the most important part of size-selective predation takes place. The average annual-decay-factor for the entire decade is actually lower, $30^{-0.1}$ = 0.712, but this is not important in the present

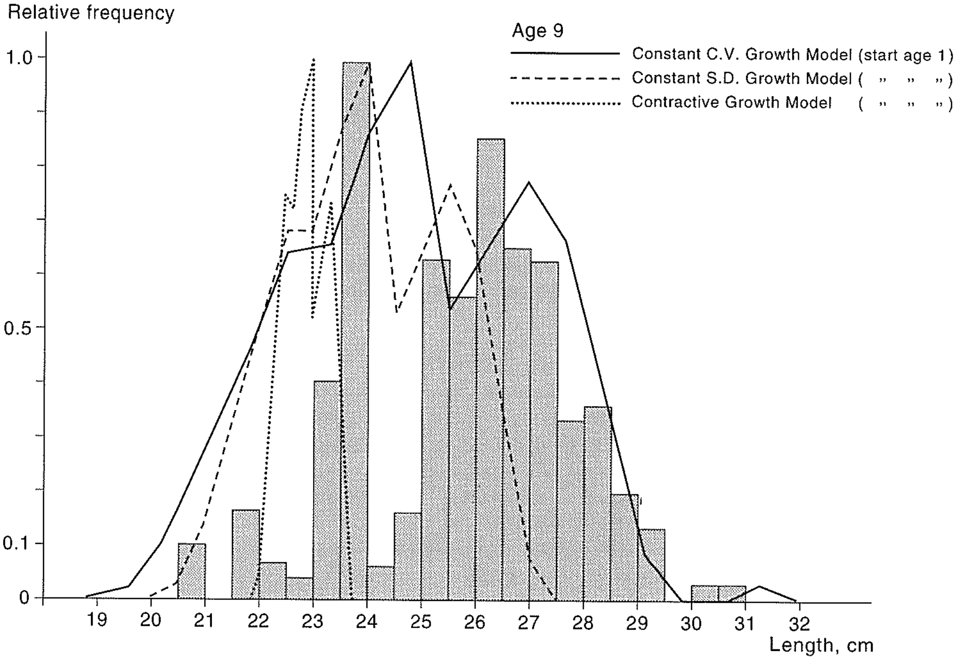


Figure 11. Length distributions of the 1981 herring year-class in October 1990 obtained after 8 years of simulation with the three growth models ($K = 0.17 \text{ y}^{-1}$, $\bar{L}_{r\infty} = 25$ cm and $\bar{L}_{r1982} = 15.25$ cm) in the estimated real-time mortality regime. Details are given in Table 3. The distributions have been scaled to a maximum value of one for comparison. The histogram is the observed length-at-age from the international acoustic trawl surveys.

context since the correct annual Q4-predation-level is controlled by P(year) in Eq. 18 where year now refers to simulation-year.

Figure 11 shows the length distributions at age 9 according to the three growth models. It appears that the Contractive Growth Model cannot account for the variability in the observed length-at-age. The Constant S.D. Growth Model also appears to give an inadequate description of data in the context here although it does almost explain the right order of magnitude in variability in length-at-age. The right-hand part of the distribution resulting from the Constant C.V. Growth Model appears to give a sensible explanation of lengths above the mean-length-at-age. However, the left tail of this distribution accounts for more small fish than what is actually represented by the histogram (data). Details on these three basic simulations are given in Table 3 (next page) together with the results of the Constant C.V. Growth Model under the sustained 1982-mortality regime shown in Figure 7A. The effect of the 1992 predation-level is negligible implying that the last column in Table 3 represents mean (somatic) growth. The effect of the high sustained 1982-level is an increase in the mean length in 1992 (after 10-years simulation at age 11) of 1.9 cm or 7.8% which in VBGE-terminology basically shows up as a similar increase in the estimate of $\bar{L}_\infty$. This is in contrast to the consequences of the real-time mortality

Table 3. Specification and characteristics of five 10-years simulations of growth of the 1981 herring year-class (see last column) under the estimated total and real-time mortality regime and starting with the observed lengths-at-age on 1 October, 1982 (e.g. $\bar{L}_{1982}$ = 16.05 cm and s.d.$_{1982}$ = 1.57 cm cf. Table 1). The first three simulations are governed by the Contractive-, the Constant S.D. – and the Constant C.V. Growth Model, respectively. The initial reference mean length, $\bar{L}_{r\,1982}$ = 15.25 cm is 0.8 cm below the mean length in the year-class, which is why $\bar{L}_\infty$ differs from $\bar{L}_{r\infty}$ in the Constant S.D. and Constant C.V. models (in the absence of size-selective mortality). The last two simulations are governed by the Constant C.V. Growth Model and the predation mortality is maintained at a sustained 1982-level and a sustained 1992-level, respectively. Estimates of VBGE-parameters, $\hat{K}$ and $\hat{L}_\infty$, are from Chapman plots (using the 10 annual mean-length increments). Unbiased estimates are only obtained in case of the negligible effect of the 1992-level of predation mortality (last column). In the other cases the calculated lengths, $\bar{L}_{\text{year}}$, representing empirical growth curves, are influenced by size-selective mortality and do not pertain to VBGE.

	SIMULATIONS					DATA
Mortality regime:	Estimated			Sustained		
	1982-92	1982-92	1982-92	1982 level	1992 level	1981 year class
IBGM:	Contractive	Constant S.D.	Constant C.V.	Constant C.V.	Constant C.V.	
$\hat{K}$	0.17	0.17	0.17	0.17	0.17	
$\bar{L}_\infty$	25.0	25.8	26.3	26.3	26.3	
$\bar{L}_{r\infty}$	25	25	25	25	25	
$\bar{L}_{r\,1982}$	15.25	15.25	15.25	15.25	15.25	
$\bar{L}_{1982}$	16.1	16.1	16.1	16.1	16.1	16.1
$\bar{L}_{1983}$	17.7	17.9	18.0	18.1	17.6	18.2
$\bar{L}_{1984}$	19.0	19.4	19.7	19.7	19.0	19.1
$\bar{L}_{1985}$	19.9	20.6	21.0	21.1	20.1	20.6
$\bar{L}_{1986}$	20.8	21.5	22.0	22.3	21.1	20.7
$\bar{L}_{1987}$	21.4	22.3	22.9	23.2	21.9	
$\bar{L}_{1988}$	22.0	23.0	23.7	24.0	22.6	
$\bar{L}_{1989}$	22.5	23.5	24.3	24.7	23.1	
$\bar{L}_{1990}$	22.9	24.0	24.8	25.3	23.6	25.7
$\bar{L}_{1991}$	23.2	24.4	25.3	25.8	24.0	
$\bar{L}_{1992}$	23.5	24.7	25.6	26.3	24.4	
$\hat{K}$	0.209	0.198	0.192	0.174	0.171	
$\hat{L}_\infty$	24.5	26.1	27.3	28.4	26.3	
s.d.$_{1983}$	1.32	1.55	1.70	1.70	1.72	2.55
s.d.$_{1984}$	1.11	1.54	1.81	1.80	1.86	2.53
s.d.$_{1985}$	0.931	1.53	1.90	1.88	1.97	2.49
s.d.$_{1986}$	0.785	1.53	1.98	1.95	2.07	2.36
s.d.$_{1987}$	0.662	1.52	2.05	2.00	2.15	
s.d.$_{1988}$	0.559	1.52	2.11	2.04	2.21	
s.d.$_{1989}$	0.471	1.52	2.16	2.08	2.27	
s.d.$_{1990}$	0.398	1.52	2.21	2.10	2.32	1.94
s.d.$_{1991}$	0.336	1.52	2.25	2.12	2.36	
s.d.$_{1992}$	0.283	1.52	2.28	2.14	2.39	

regime with the Constant C.V. Growth Model where the increase of 1.2 cm or 4.9% in mean length at age 11 appears as an increase in apparent K (13%) as well as in apparent L_∞ (3.8%). The s.d.-at-age continues to increase in the Constant C.V. Growth Model in contrast to the data on the 1981 year-class. The s.d. decreases slightly (2%) during the first years in the Constant S.D. Growth Model but then remains constant when the fish have reached a size and an age (year) at which the mortality effect ceases. Note that apparent growth in the Constant S.D. Model results in almost a correct estimate of $\bar{L}_\infty$ but overestimates K by 16.5%. This tendency is even more pronounced in the Contractive Growth Model. Although the effect of mortality on mean length-at-age here is as small as 1 mm at age 11, the effect on K is an overestimate of 23%.

The short-term dynamics of the Constant C.V. Growth Model is important. A major part (1/3) of the accumulated increase in mean length over the 10 years takes place during the first year in particular during the third quarter (Q3) of 1983 with its high level of predation mortality. However, by disregarding the seasonal variation in the predation mortality, the mean length actually increases slightly during the very first quarter (not shown). The reason is that Q3 is the last quarter in a simulation year. Thus the effect of transferring mortality from Q3 to the other quarters is an increase in apparent growth because the fish are smaller and hence exposed to more size-selection. After 10 years of simulation without seasonality in the predation mortality the mean length (at age 11) becomes 25.69 cm or only 1 mm greater than with seasonality (Table 3). The effect of including seasonality in growth is also small yielding $\bar{L}_{1992} = 25.72$ cm when K is doubled in the second and third quarter and put to zero in the first and the last quarter of the calendar year (not shown). Possible changes in the mode of the length-distribution are also of interest. The mode of the length distribution on the starting day (1 October 1982) is 15.25 cm (cf. Table 1). This length group is, of course, still the mode at the end of the first year (16.77 cm) in case of non-size selective mortality (e.g. the 1992 situation). In all the other cases the mode shifts three classes up (18.42 cm) due to the effect of size-selective predation in the first year (not shown).

The longer-term effects (Figure 12) shows that the Constant C.V. Growth Model is not able to account for the variability in length during the first couple of years when the start distribution is lengths at age 1 in 1982. Using instead lengths at age 2 in 1983 (i.e. the histogram in Figure 12A) as the start distribution, the Constant C.V. Growth Model and the Constant S.D. Growth Model produce almost identical length distributions one year later in 1984 (Figure 12B; only distribution for Constant C.V. Model is shown). The distributions explain the left part of the histogram but account relatively for too many big fish. Thus the problem is now reversed. The models overestimate the variability in length-at-age. Continuing these simulations for six years produces Figure 13 for the situation on 1 October 1990. Both models greatly overestimate the relative number of small fish. The Constant C.V. Growth Model also overestimates the frequency of big fish and, hence, cannot explain the observed histogram in case of lengths at age 2 as start distribution. The Constant S.D. Growth Model appears to offer a sensible explanation of the right tail of the histogram. These simulations were generated with $K = 0.16$ y^{-1}, $\bar{L}_{r\infty} = 25$ cm and $\bar{L}_{r1983} = 16.75$ cm

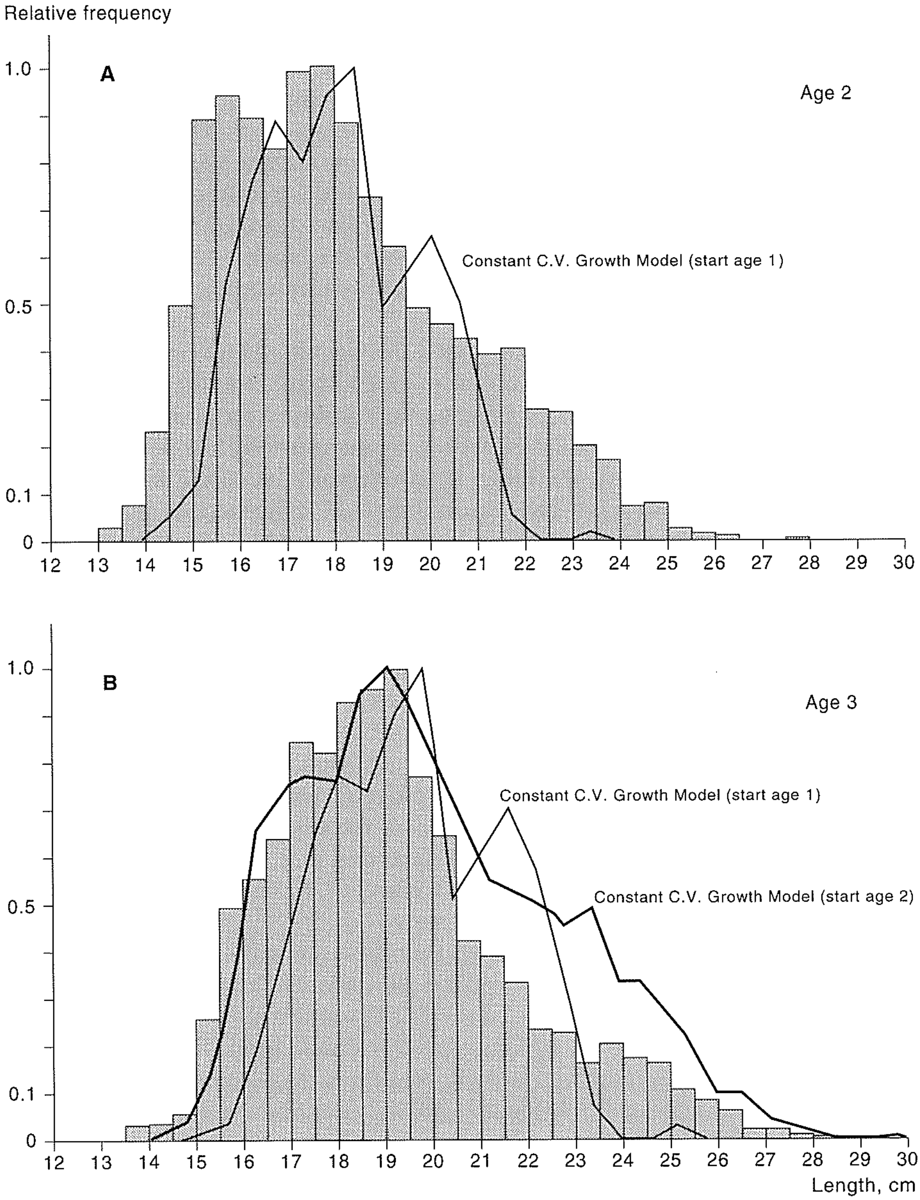


Figure 12. Length distribution of the 1981 herring year-class in A: October 1983; and B: October 1984 after 1 and 2 years simulation with the Constant C.V. Growth Model ($K = 0.17\ \mathrm{y}^{-1}$, $\bar{L}_{r\infty} = 25$ cm and $\bar{L}_{r\,1982} = 15.25$ cm). The 6-years continuation of this simulation is depicted in Figure 11. The histograms are from the acoustic trawl surveys (Table 1). The heavy solid curve in 'B' is the length distribution of the histogram in 'A' after 1-year simulation with the Constant C.V. Growth Model ($K = 0.16\ \mathrm{y}^{-1}$, $\bar{L}_{r\infty} = 25$ cm and $\bar{L}_{r\,1983} = 16.75$ cm). The total mortality in operation is in accordance with the estimated trawl selection ogive and the estimated size-selective predation mortality by year and quarter.

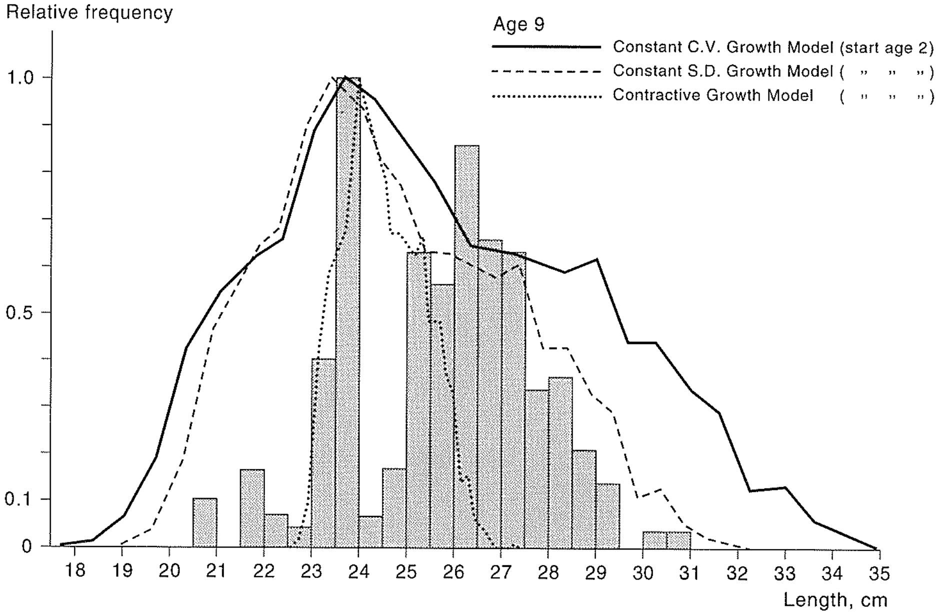


Figure 13. Length distributions of the 1981 herring year-class in October 1990 obtained after 7 years of simulation with the three growth models ($K = 0.16\ y^{-1}$, $\bar{L}_{r\infty} = 25$ cm (but 27 cm in Contractive VBGE Model) and $\bar{L}_{r\,1983} = 16.75$ cm) in the estimated real-time mortality regime. The start distribution is the histogram in Figure 12A (age 2). The distributions have been scaled to a maximum value of one for comparison. The histogram is the observed length-at-age from the international acoustic trawl surveys.

where the latter equals $\bar{L}_{r\,1982} = 15.25$ cm after one year of growth at $K = 0.17\ y^{-1}$. Figure 13 also shows the length distribution of the Contractive Growth Model under the same conditions but with L_∞ raised by 2 to 27 cm. The left tail of this distribution appears to be able to account for the steep build-up of the histogram. However, this Contractive Growth Model still cannot explain the variability in length-at-age.

5. Discussion

The effect of size-selective mortality on size-at-age has long been recognized and dates back to the well-known Lee's phenomenon (see Ricker 1969, 1975 p. 125). Nevertheless, the implications of variations in size-at-age have largely been ignored in fish stock assessment. This is usually reduced to a table of fixed mean weights-at-age. Apparently exceptional events or very drastic changes in the overall abundance of fish stocks are needed to disturb this stability in mean weight-at-age. However, it is to be expected that the Baltic with its one-way food-chain, cod eating herring and sprat, is likely to show signals of changes in size-at-age at an early stage compared to systems such as the North Sea that are driven and stabilized by a complex and dynamic interplay between many piscivorous and opportunistic fish species. For example, Popiel (1958) observed a distinct increase in the size of autumn spawning herring from the Bornholm Basin from the 1930s to the 1940s and

1950s which actually coincided with a steep increase in the cod landings (Sparholt 1994). The recent decrease in size-at-age of herring coincides with the collapse of Baltic cod and it is against this background that the present study attempts to deal with a consistent quantification of the effects of size-selective predation on size-at-age in continuation of the work by Sparholt & Jensen (1992).

5.1. *The quantification of individual growth of herring*

The three IBGMs are based on VBGE and isometric growth, i.e. using body-weight

$$\mathrm{d}W/\mathrm{d}t = HW^{2/3} - kW\,; \qquad W = qL^3 \tag{20}$$

The classical interpretation of this VBGE, first formulated by Pütter (1920), is that growth equals the difference between (surface-dependent) food uptake and (volume-dependent) break-down. The rationale underlying VBGE is in this way related directly to the individual fish but in most applications Eq. 20 (with W replaced by $\overline{W}$) is used to describe mean growth-at-age hereby assuming that all fish in the cohort are of the same size (e.g. Beverton & Holt 1957). Other metabolic growth models (e.g. Ursin, 1967, 1979) merely differ with respect to the powers in the terms for anabolism and catabolism. In such simple descriptions of growth all costs related to food uptake are considered incorporated in H, the coefficient of anabolism implying that K specifies the coefficient of fasting metabolism. In the North Sea Model, Andersen & Ursin (1977) in describing mean growth in a cohort (age group) considered H to be proportional to the feeding level which at any point in time was determined by the availability of food for the age group. This makes growth a dynamic process in contrast to the stationary description in Eq. 20 with constant H.

In the present paper a cohort is considered to comprise fish of different sizes. The original interpretation of H and k is maintained and Eq. 20 shows how L_∞ and K are related to these parameters, i.e.

$$\mathrm{d}L/\mathrm{d}t = K(L_\infty - L)\,; \qquad K = k/3\,; \qquad L_\infty = q^{-1/3}\,H/k \tag{21}$$

In all three IBGMs, K is assumed to remain constant within the cohort and the observed variation in size-at-age is explained by the individual variation in L_∞ and/or in the time of hatching. If an extensive spawning season represents the only cause of future variation in growth then individual growth should be governed by the same (reference) L_∞, i.e. the Contractive Growth Model. The Constant Variance Growth Model and the Constant C.V. Growth Model represent two different formulations in which at least part of the variability in size-at-age is considered to be accounted for by variations in the $L_{\infty\mathrm{ind}}$'s and hence by variations in the growth rates-at-length. It follows from Eq. 21 that L_∞ is directly proportional to H because k is considered constant.`Thus the interpretation of a $L_{\infty\mathrm{ind}}$ is that each fish is associated with a H_{ind} which is considered to remain constant during its entire life-span. The possible causes of such a distribution of individual H-values has not yet been considered . It is likely that those fish which by random chance in early life were able to encountering and successfully eating copepod nauplii at a more frequent rate than on average will continue to grow at a sustained higher rate. Such an explanation is supported by simulation studies. For example, Beyer & Laurence (1980,

1981) using a metabolic IBGM with $HW^{2/3}$ in Eq. 20 replaced by the actual daily ration resulting from random predator-prey encounters were able to explain all the variance in size-at-age that was building up when larval fish were reared in the laboratory for two months. This gave rise to an increasing c.v.-at-age with increasing age. Such stochastic models are truly IBGMs. One may argue that the present VBGE-based growth models are not IBGMs in a strict sense. However, it is of note that simple deterministic modelling is used here to gain insight into the effects of variability in size-at-age on the mean population characteristics. This does not mean that any one fish in reality is expected to grow according to a smooth VBGE but it is a simple way of modelling the variability in data on lengths-at-age.

The present models with constant s.d. or c.v. have been chosen as an operational starting point for introducing the opposite effect of the exponential reduction of s.d. in the traditional Contractive Model with fixed VBGE-parameters. Sainsbury (1980) also considered an IBGM with a pair of VBGE-parameters associated to each fish throughout life. Sainsbury uses probability distributions to describe the individual variability in K and L_∞ and then provides equations governing the mean and variance of length-at-age in the absence of size-selective mortality and assuming identical lengths initially. Such an approach is attractive from a theoretical point of view. The problem is lack of data to provide guidance on how L_∞ and K actually vary among members of a group of fish (Sainsbury 1980). It is for this reason that we have chosen to formulate the IBGMs based on the observed variation in length-at-age at some initial time.

The questions regarding whether fish mainly grow according to their size independently of their age (or cohort to which they belong) or vice versa cannot be distinguished in the Contractive Growth Model because of the one-to-one correspondence between age and size in VBGE. The Constant C.V. Growth Model invalidates this traditional principle and thus represents a mixture of these two points of view: 1) fish exhibit a growth pattern determined by the cohort to which they belong and 2) fish of different size but belonging to the same cohort may have different growth rates. Consequently, fish of the same size but belonging to different cohorts may eventual have different growth rates at a particular time of the year. This may seem unusual but empirical evidence does give some support to cohort-dependent growth for Baltic herring. Sparholt (1994) concludes from Anon. (1993) that the changes in size-at-age have been more related to year-classes than to years indicating a cumulative effect of the responsible factor.

Proper estimation procedures for (somatic) growth have not been attempted in this preliminary study. The present study concludes from the examination of the 1981 year-class that the VBGE-parameters of the mean growth of herring in subdivisions 25-29 are reasonably close to $K = 0.17\ y^{-1}$ and $L_\infty = 26$ cm. This value of K is small compared to traditional values (which, however, all relates to apparent growth rates). Otterlind (1962) observed that the growth rate of herring in the Baltic decreases towards the north. In terms of K the decrease is from 0.54 to 0.25 (Ojaveer 1981). However, in a more recent study, Parmanne (1988) found the opposite trend in the northern Baltic, i.e. K increasing from 0.25 (varying between 0.13 and 0.40) in subdivision 29 to 0.30 in the Bothnian Sea (subdivision 30) and

0.43 in the Bothnian Bay (subdivision 31). L_∞ appears to decrease by ca. 6 cm towards north and our value is in accordance with other observations for subdivisions 25 to 29 (e.g. Ojaveer 1981, Parmanne 1988).

5.2. *The quantification of predation by cod on herring*

It may be anomalous that the predation mortalities in Figure 5A for subdivisions 25-27 in 1982-92 show increasing variation with increasing size up to length ca. 24 cm (i.e. $\ln W_{[\mathrm{kg}]} \simeq -2.5$). The mortalities vary by a factor of ca. 150 in the 5-cm range around 24 cm whereas the variation in the smallest length range, 10-15 cm, represents only a factor of ca. 20. One would expect the opposite trend in residual variation if size alone was able to explain most of the mortality variation because of presumably less precision in MSVPA-data for small herring and the influence of sprat. However, one could also expect increasing $M2$-variability with increasing prey length to reflect the fact that larger prey are found rather infrequent in the cod stomach data (constituting the basis for the calculations in the MSVPA). The allometric model in Figure 5A, $M2 \propto L^{-3.74}$, must be rejected explaining only 22% of the variance. The estimated power (-1.25 in the $M2$-W relationship) is significant but this fact alone is misleading when the aim is to derive an analytical predation model that can describe $M2$-at-size. Sparholt & Jensen (1992) included sprat and obtained a power of -3.0 in a similar analysis of $M2$-at-L for the years 1982-88 ($r^2 = 40\%$).

In explaining the mortality variation, cross-effects were not marked compared to the significance of the seasonal and annual factor-effects. The highest level of predation occurs in the third quarter of the year which also is the most important feeding season for herring (Voipio 1981). The level of size-specific predation mortality has dropped by a factor of 30 from 1982 to 1992. This fact is not in conflict with the accepted situation that the predation mortality has decreased by only 70% during 1982-92 (e.g. Anon. 1994). The 70% refers to the decrease in age-specific mortality, $M2_{\mathrm{age}}(t)$, and thus does not take the simultaneous decrease in size-at-age into account. The average decrease in the size-specific mortality, $M2_{\mathrm{length}}(L)$ or $M2_{\mathrm{weight}}(W)$, is 96.67% or a factor of 30. The importance of distinguishing between M_{age} and M_{size} in survival analysis is discussed by Beyer (1989). Figure 6 shows that the level of predation mortality is proportional to the cod spawning stock biomass as first noted by Anon. (1992). Although not surprising the closeness of fit in such a relationship is not given from the outset. MSVPA uses stomach evacuation models (and not directly cod weight-at-age) to transform stomach contents into estimates of food-consumption in the iterative determination of numbers-at-age.

After removing the annual and seasonal contributions, Figure 5B shows that the mortalities lie within a narrow range (in which the maximum range of variability has been reduced by more than a factor of 50) around the allometric model which states

$$M2_{\mathrm{size}} \propto W_{\mathrm{her}}^{-1.722} \propto L_{\mathrm{her}}^{-5.165}$$

The numerical power has increased significantly and its s.e. has been reduced by more than a factor of 3. It is of value to consider the consequences of this mortality-length relationship in terms of mass balance and size-preference by cod in the predation process. Proceeding as in Beyer (1989, Example 10) but using VBGE-terminology for the rate of food-consumption by cod, mass balance requires

$$N_{\mathrm{cod}}\, W_{\mathrm{cod}}^{2/3} \propto M2_{\mathrm{size}}\, N_{\mathrm{her}}\, W_{\mathrm{her}}$$

where the Ns refer to numbers-at-size. If this relationship instead expresses the size-specific balance between many predators and prey species such as in the North Sea and assuming that a predator prefers to eat prey of a specific fraction of its own size (Andersen & Ursin 1977) then W_{pred} is proportional to W_{prey}. In a steady-state biomass spectrum N_{pred} is then proportional to N_{prey} and the Ns disappear in the mass balance. The relationship is thus reduced to $M2_{\mathrm{size}} \propto W^{-1/3} \propto 1/L$ supported by examinations of the predation mortalities-at-size governing the North Sea (Anon. 1991). This explains why one might have expected a power, p, in the order of one and not five in the present study. However, the dynamics of the specific cod-herring signal in the Baltic must be treated differently. In a first approximation the increase in N_{her}-at-age and the decrease in W_{her}-at-age caused by the collapse of cod in the 1980s produces a constant N_{her}-at-size during the 1980s. This approximate balance is a direct consequence of simple size-specific analysis (Beyer 1989) because if age-specific recruitment increases then so will size-specific recruitment and if K and/or L_∞ decreases at the same time then so will number-at-size. Furthermore, considering the size-frequency distribution of mature cod constant (which actually is supported by Danish cod trawl surveys, own obs.), the SSB of cod is proportional to the biomass-at-size and we may write

$$M2_{\mathrm{size}} \propto N_{\mathrm{cod}}\, W_{\mathrm{cod}}\, W_{\mathrm{her}}^{-1.722}$$

which inserted in the relationship for mass-balance gives (assuming isometric growth for cod as well),

$$W_{\mathrm{cod}}/W_{\mathrm{her}} \propto W_{\mathrm{her}}^{1.166} \propto W_{\mathrm{cod}}^{0.538} \propto L_{\mathrm{cod}}^{1.615}$$

The interpretation is that Baltic cod in subdivisions 25-27 on average eat herring in a predator/prey weight-ratio which is not constant but increases with increasing predator size. Bundgaard & Sparholt (1992) reached the same conclusion working directly with length distributions of herring in cod stomachs relative to the length distribution of herring in the sea. Fitting an allometric model to their estimates of the optimal predator/prey size-ratio (their table 5) gives a similar result: $W_{\mathrm{cod}}/W_{\mathrm{her}} = 0.1328\, L_{\mathrm{cod[cm]}}^{1.626}$ ($r^2 = 0.89$). Taking the cube-root of this equation (assuming the same condition factor for cod and herring) we obtain, for example, that cod of 85 cm length prefer herring of length 15 cm (i.e. weight-ratio ca. 180) whereas cod of 35 cm length prefer herring of 10 cm length (i.e. weight-ratio ca. 40).

The size-specific predation mortality in Eq. 18 has been obtained indirectly from age-based MSVPA. Variability is introduced at many levels due to various size-to-age and age-to-size transformations involved. The main purpose has been to demonstrate that the key information contained in MSVPA can be expressed by simple means. A more elaborated analysis requires a critical examination of errors involved in the averaging processes. For example, size-selective predation will make the mean weight-at-ingestion-at-age smaller than the mean weight-at-age in the population which again will be smaller than the mean weight-at-age in the catch due to the opposite trend in the size-selective fishing mortality. The mean weights in the catch used (incorrectly) in Figure 5 are larger than the (unknown) mean weights at ingestion which would have been more appropriate. However, reducing the weights would increase the numbers required to explain food-consumption and MSVPA would then produce higher predation mortalities. The data for Figure 5, in particular for the smaller herring in the early 1980s, should thus be adjusted downwards to smaller weights and also upwards to account for the higher mortalities. Such mechanisms may explain why the same allometric mortality model appears to be valid independently of the level of predation mortality.

5.3. *The effect of mortality on the size-at-age of herring*

The impact of mortality on length frequency distributions is determined by the absolute difference in mortality within the domain of size variation. This coupled with the quantification of mortality at lengths greater than ca. 10 cm shows immediately where, when and how size-selective effects are of particular importance. In 1982 the mortality impact will be on herring with lengths from 10 to 20 cm because Figure 7A shows that the smaller fish in a year-class will disappear much more rapidly than the large ones in this length range. The predation mortality equals the fishing mortality at length 20 cm from which size onwards total mortality stabilizes and hence produces a negligible effect on size-at-age. The sustained decrease in predation during the following years causes the starting point of mortality stabilization to move towards smaller lengths. In 1992 the predation mortality equals the fishing mortality already at length 12 cm (see Figure 7B) and the mortality effect on size-at-age is negligible over the entire size range. The investigations have also shown that the long-term effects of seasonality in growth and predation can be neglected in the present context. The conclusion in relation to the 1981 year-class is that the major impact of mortality on size is caused exclusively by predation and (apart from 1981) took place in 1982 and to a lesser degree in 1983. The following discussion of the mortality effect on the dynamic of size-at-age can therefore be related to the size-specific dynamics of predation in about 1982.

The rate of increase in mean length caused by predation is in a first approximation determined by the variance in length multiplied by the differential mortality by length that may be considered proportional to $L^{-(p+1)}$, the slope of the size-specific mortality curve. This relationship will only be exact if mortality bears a linear relationship to length, $p = -1$, in which case the mortality does not cause s.d. to change (Jones 1958). It is instructive to reconsider Figure 9 in view of this relationship. The increase in mean length during the first year more than triples (from 3.7% to 12.3%) when the initial s.d. doubles from 1.5 to 3 cm. This simple example illustrates three important points. Firstly, the s.d. ratio is reduced from 2 to 1.7 during the first year which explains why the bias in observed mean growth increases by a factor of $3.3 \sim 1.7^2$ rather than by 4. Secondly, most of the fish surviving the first year have grown into the stable mortality regime implying that the mortality effect on size virtually ceases after the first year. This is not surprising as the mortality effect is reduced by a factor of $1.50^{6.165}$ or 12 when the mean length increases by

50%. The third point offers a simple explanation to the decrease in the weight of Baltic herring. Removal of the 1982-predation level in the example causes the mean weight to decrease by 10-30% during the first year (for initial s.d. between 1.5 and 3 cm). The impact of mortality on the length of herring at age 2 and older depends very much on the mean and s.d. of lengths at age 1. This point is best discussed further in relation to the examinations of the 1981 year-class.

Size-selective predation can explain an average decrease in mean weight-at-age during the 1980s of ca. 10% for age 2 which gradually increases to ca. 20% at old age (Table 3). This pattern is also revealed in the data in Figure 2 which (using non-linear estimation of the VBGE-parameters for the 1980-82 and the 1990-92 situations separately) give the average decrease as 15% for age 2 increasing to 25% at old age (see also mean weights at age in year-classes 1974-91 in Anon. 1993 or Sparholt 1994). Apparently the correct trend of decrease in mean length-at-age can be simulated with the Constant C.V. Growth Model. The lower growth rate (mainly caused by $K = 0.17\ y^{-1}$ in Table 3 compared to $K = 0.3\ y^{-1}$ in e.g. Figure 9) extends the time frame of the mortality effect by one year. Once the smaller fish with low growth rates have disappeared the bigger ones continue to grow fast in the model. Thus a small decrease in mean length at age 1 on 1 October (i.e. 1 cm) and a corresponding small increase in s.d. (i.e. ca. 0.5 cm) will bring the effect of mortality on mean size up to the observed level. Indirect evidence exists to such an effect. The hydroacoustic surveys do not show decreasing mean size at age 1 during the 1980s (own obs.) and neither does the weights-at-age used in MSVPA (Anon. 1993, Sparholt 1994). However, a decreasing trend should be expected in the mean size due to a decrease in (unknown) size-selective predation during the first year of life. One explanation is that the inshore population of herring smaller than 10 cm is not fully represented in neither surveys, sampled stomachs nor the catch. The missing herrings will then be recruited at length ca. 10 cm to the deep basins after 1 October the effect of which must be accounted for in the present model by changing the initial distribution in Table 1 towards the initial situations in Figure 9 such as $N(15,2^2)$. In the model the effect will also be an initial difference between observed and reference mean sizes at age 1 (Figure 10) that will diminish during the 1980s. The magnitude of the decrease in mean size-at-age during the 1980s is sensitive to such size-selective effects occurring in the juvenile stages. In view of all the uncertainties involved (including the problems of interpreting observed or apparent growth data on mean size-at-age correctly), the hypothesis cannot be rejected that the decrease in the size of herring is caused by predation. This leads to the next issue concerning errors in obtaining the VBGE-parameters of (somatic) growth from (observed) apparent growth.

Caution is required in estimating VBGE-parameters of apparent growth by the traditional methods. For example, the conclusion (Figure 9) that a sustained 1982-predation level leads to an increase in both parameters is an artefact because the last two columns in Table 3 show that the real effect basically is an increase in $\bar{L}_\infty$ only. The problem is that apparent growth does not follow VBGE even though good relationships are obtained. Precise estimates of the parameters can only be obtained based on few years data when these pertain to VBGE. If not, the Chapman plot results in a high overestimate of K unless a long time-series is available (Table 3). This also shows in the data. The Chapman plot based on the four annual mean-length increments (derived from Table 3, last column) produces $K = 0.50\ y^{-1}$ and $L_\infty = 21.5$ cm. Estimation based on the weight data in Figure 2 for various time-periods or year-classes also produce values of K in excess of 0.5. However, the appropriate order of magnitude for K in describing length-at-age of the 1981 year-class is only 0.2. Due to the real time mortality regime, this K-estimate must further be reduced by ca. 15% to 0.16-0.17 to describe the real K in the Constant C.V. Growth Model. This K-bias increases to 25% in the traditional (Contractive) Model because L_∞ cannot increase.

None of the three growth models can explain the variability in length-at-age over the entire life-span of the 1981 herring year-class. The Constant C.V. Growth Model appears to capture several of the features in the shape of the observed length frequencies (e.g. the fluctuations in the histogram for herring longer than 23 cm at age 9 in Figure 11). However, the smaller herring grow too slowly in the Constant C.V. Model. We reject the Contractive Model which operates with the same VBGE-parameters for all members of the cohort. Even if smaller herrings are not fully accounted for at age 1 in the October 1982 sample (as discussed above), these herrings should be present in the sample one year later (Figure 12A) but the Contractive Model advanced from here can still not account for the variability in length at old age (Figure 13). The data in Table 1 shows that s.d.-at-age increases from age 1 to age 2 and then continues to decrease slowly. Ricker (1969) cites examples with populations of sprat and bluegill sunfish that show the same trend and interprets the phenomenon as growth compensation, i.e. the tendency for the smaller fish to catch up with the larger ones. Size-selective mortality cannot quite explain the decrease in variance of length with increasing age in the Constant S.D. Growth Model (Table 3). This fact is also shown in Figure 13 in which K has been reduced by ca. 5% from age 2 onwards to account for part of the spawning losses that are not taken into account by Eq. 20. A combination of the fast catching up effect for the smaller ones in the Contractive Model (i.e. its left tail) with continued growth in length of the bigger and mature ones (although at a reduced rate) according to the Constant S.D. or C.V. Models (i.e. their right tails) seems to produce the correct tendencies to match the histogram in Figure 13. It indicates that more elaborated IBGMs are needed which incorporate size-specific changes in the growth pattern at maturation.

The investigations of growth in this study are of preliminary nature and clearly warrant an in depth study based on complete data of size-at-age for individual fish (by back-calculations from scales or otoliths) as well as for the 1980-90 year-classes on a subdivision-basis in order to arrive at definite conclusions. It is of particular importance to begin utilizing the information on growth patterns contained in the variability of size-at-age. Growth compensation does occur in some cases but many fish species show increasing s.d.-at-age with increasing age (e.g. Sainsbury 1980 and references herein). Is Baltic herring one of them or has the s.d.-pattern changed during the 1980s? The answers to such questions constitute an essential prerequisite of quantifying the impact of mortality on mean size-at-age. The hypothesis that the growth of herring has remained constant during the 1980s cannot yet be rejected. Mortality alone may constitute the responsible factor for the decrease in mean size-at-age of Baltic herring but other causes are still disputed (Sparholt 1994).

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