

**MODELLING AGE-DEPENDENT NATURAL MORTALITY OF
JUVENILE NORWEGIAN SPRING-SPAWNING HERRING
(*Clupea harengus* L.) IN THE BARENTS SEA**

by

P. de Barros¹ and R. Toresen

Institute of Marine Research
P.O.Box 1870, N-5024 Bergen

¹ Universidade do Algarve, Campus de Gambelas
P.O.B. 322 - 8004 FARO PORTUGAL

ABSTRACT

Understanding the patterns of mortality in the juvenile stages is essential for improving current stock assessment procedures. A crucial aspect is at which stage in the life cycle of fish is year-class strength determined. Most of the research on "the recruitment problem" has focused on the larval stages, but recent work indicates that a large part of the variability in year-class strength may be associated with variable mortality during the juvenile stages. A statistical model, including age and year-class effects, was built, and fitted to the data on abundance of juvenile Norwegian spring-spawning herring in the Barents Sea collected by the Bergen Institute of Marine Research between 1983 and 1993. The results indicate that mortality is strongly age-dependent, and that most of it occurs during the first year of life. There is also a large inter-cohort variability in juvenile survival. Survival from the start of the 0-group stage to age 3 years may have varied from very low to around 30% for the cohorts investigated..

INTRODUCTION

Most of the natural (non-fishing) variability in fish population abundance is associated with recruitment (Sissenwine 1984), but recruitment variability remains the single least understood problem in fisheries science (Houde 1987). Most fishes are extremely fecund, and by the time a cohort recruits to the fishery, its abundance will typically have been reduced by several orders of magnitude (Cushing 1974). Among the pre-recruit stages, it is in the larval stages that mortality rates are highest, and small changes in these rates have the potential to account for large changes in recruitment (Wooster and Bailey 1989).

In this framework, it is hardly surprising that most studies of recruitment variations are still based on Hjort's (1914) hypothesis that year-class strength is determined in the early larval

stages (Wooster and Bailey 1989). Recently, it has been suggested that a) variable mortality during the juvenile phase may account for a large part of the observed variability in recruitment (Sissenwine 1984 1986; Smith 1985; Daan 1987; Sparholt 1990; Fogarty *et al.* 1991) and b) this mortality should be strongly size- (and age-) dependent (Vetter 1988; Beyer 1989; Caddy 1991).

Despite several studies on this variability, there have been very few studies which have convincingly demonstrated the existence of appreciable inter-cohort variability in juvenile survival. Also, we know of none, other than those based on MSVPA (Sparholt 1990), showing that this mortality is size- or age-dependent. This is in most cases due to the difficulty in separating variable mortality from errors in the abundance estimates. To actually demonstrate the existence of changes in mortality rate with age or cohort, it is thus necessary to explicitly account for these errors, including them in the modelling procedure.

The Norwegian spring-spawning herring stock is one of those with largest recruitment variability in the Northeast Atlantic (Dragesund 1970; Serebryakov 1991), and it is often dominated by a couple of strong year-classes. In periods of low stock abundance, recruitment of a single good year-class may more than double the spawning stock biomass. Exceptional year-classes seem to occur only in years when a large part of the juveniles are distributed in the Barents Sea area (Dragesund 1970; Østvedt 1958; Seliverstova 1990a 1990b). The fish whose nursery is located in this area have a long juvenile period (3 years), meaning that recruitment will be quite sensitive to changes in mortality rate at this stage. It is therefore one of the most suitable stocks for testing whether variable juvenile survival may significantly affect year-class strength, measured at recruitment to the adult stock.

In this work, we develop a statistical model for abundance-at-age, which allows for age- and cohort-dependent mortality. This model is fitted to the series of abundance estimates of young herring in the Barents Sea collected by the Institute of Marine Research in Bergen (IMR) between 1983 and 1994 (Toresen and Barros 1995). The fit of the model to the data is analysed to test the null hypotheses that 1) the observed inter-cohort variability in juvenile mortality can be attributed to measurement errors and 2) mortality through the juvenile period is constant. For use in stock assessment work and for later investigations, we also present estimates of the actual mortality levels experienced by the different cohorts in the data set, and investigate the precision of these estimates.

MATERIAL AND METHODS

The data

The work presented in this paper is based on an analysis of a series of acoustic abundance estimates of pre-recruit herring in the Barents Sea nursery area collected between 1983 and 1984 as a part of the routine surveys undertaken in this important fishery area by IMR, which are presented and discussed by Toresen and Barros (1995). These estimates cover the juvenile period of the herring year-classes 1983 to 1993, with the exception of the year-classes 1986 and 1987, which recruited in so low numbers to the 0-group stage that they were taken as non-existent in the Barents Sea (Anon. 1994a).

The age of the herring corresponding to each estimate was calculated by computing the time interval (in years) between the assumed hatching date and the date assigned to the estimate. It

was assumed that all fish in one cohort hatched simultaneously in April 1st. This choice of the hatching date was based on a study of hatching curves (Fossum 1993).

Not all estimates are equally reliable. Problems arising during some surveys led to estimates which are recognised as having a poorer quality than the others. However, they still convey important information, and were included in the analysis. To reflect their lower reliability, they were downweighted, by being assigned a relative "external weight" of 0.75. (Figure 1). The "external weight" assigned to the other estimates was 1.

The model

The research work done during the last decades has established that the young stages of fish suffer, in general, by a pattern of high instantaneous mortality rate, M , declining rapidly as the fish grow older, and achieve a relatively stable level as the fish approach maturity (Beyer 1989; Caddy 1991; Vetter 1988; McGurk 1993). The instantaneous mortality rate M may thus be modelled as a function of age and denoted $M(t)$.

In this study, the Pareto function (Arnold 1985) has been used to model the relationship between M and age. This means that the expression for M at age t , $M(t)$, may be written

$$M(t) = M_{\infty} + \beta t^{-\alpha} \quad (1)$$

where M_{∞} is the mortality rate at (theoretical) infinite age, β is the difference between mortality at age 1 and asymptotic mortality, and α is a 'shape parameter', defining how fast the mortality change from the high mortality level typical of the young stages to the relatively stable and lower mortality of the adults. This model is able to reproduce most of the patterns of M -at-age considered for this phase of life, from a constant mortality ($\beta=0$) to a rapidly declining mortality to a stable level. This equation may be reparametrized to consider the mortality at the start age, $M(t_0)$ as a parameter rather than at age 1, becoming

$$M(t) = M_{\infty} + (M_{t_0} - M_{\infty}) \left(\frac{t}{t_0} \right)^{-\alpha} \quad (2)$$

where M_{t_0} is the mortality rate at age t_0 , and the other parameters are as described above.

Specifying $M(t)$ by expression (2), survival between ages t_0 and t_1 becomes

$$S(t_0, t_1) = \frac{N(t_1)}{N(t_0)} = e^{-\int_{t_0}^{t_1} M(x) dx} = \begin{cases} e^{-\left[M_{\infty}(t_1 - t_0) + \frac{(M_{t_0} - M_{\infty})t_0}{1-\alpha} \left(\left(\frac{t_1}{t_0} \right)^{1-\alpha} - 1 \right) \right]} & \text{if } \alpha \neq 1 \\ e^{-\left[M_{\infty}(t_1 - t_0) + (M_{t_0} - M_{\infty})t_0 \ln \left(\frac{t_1}{t_0} \right) \right]} & \text{if } \alpha = 1 \end{cases} \quad (3)$$

And the abundance of the cohort at age t , $N(t)$ may therefore be written as

$$N(t_1) = \begin{cases} N(t_0)e^{-\left(M_\infty(t_1-t_0) + \frac{(M_{t_0} - M_\infty)t_0}{1-\alpha} \left(\left(\frac{t_1}{t_0}\right)^{(1-\alpha)} - 1\right)\right)} & \text{if } \alpha \neq 1 \\ N(t_0)e^{-\left(M_\infty(t_1-t_0) + (M_{t_0} - M_\infty)t_0 \ln\left(\frac{t_1}{t_0}\right)\right)} & \text{if } \alpha = 1 \end{cases} \quad (4)$$

expressing the expected number of survivors at age t_1 , $N(t_1)$, as a function of the number initially present $N(t_0)$, the initial age t_0 and M_∞ , M_{t_0} and α .

Model (4) describes the abundance-at-age for one cohort. Stronger inferences can be made by using a model which can be fitted simultaneously to all cohorts in the data set, since this will allow us to make use of the regularities in the survival patterns among cohorts in the estimation process. Mortality experienced by the herring during the juvenile stages will most probably depend on the absolute abundance of its predators, on the relative sizes of the herring and the predators and on the degree of geographical overlap among the two. While the first of these factors varies from one year to the next, the two latter have a strong seasonal character. It is thus reasonable to assume that the level of mortality experienced by the different cohorts will vary, but that the pattern of decline in this mortality with age will be more or less the same for all cohorts. After recruiting to the adult stock, they will all more or less share the same environment, and will be subjected to the same conditions. Model (4) may thus be generalized by

$$N_c(t_1) = \begin{cases} N_c(t_0)e^{-\left(M_\infty(t_1-t_0) + \frac{(M_{t_0g} - M_\infty)t_0}{1-\alpha} \left(\left(\frac{t_1}{t_0}\right)^{(1-\alpha)} - 1\right)\right)} & \text{if } \alpha \neq 1 \\ N_c(t_0)e^{-\left(M_\infty(t_1-t_0) + (M_{t_0g} - M_\infty)t_0 \ln\left(\frac{t_1}{t_0}\right)\right)} & \text{if } \alpha = 1 \end{cases} \quad (5)$$

This model considers a different start number and a different mortality level for each cohort. The pattern of decline in mortality with age (represented by α) and the asymptotic mortality M_∞ are assumed to be common for all cohorts. If at least some cohorts have experienced so similar mortalities that they can be treated as if they had followed the same survival curve, the model can be simplified further by forcing these cohorts to share the same M_{t_0} parameter. In the model above, c and g index, respectively, each cohort and each group of cohorts assumed to have followed the same survival curve.

This model can now be used as a tool for investigating (1) which cohorts can be taken as having suffered at least approximately the same mortality (the null hypothesis states that all had the same mortality), (2) what kind of differences in mortality can be demonstrated with the data at hand, and (3) whether the assumption of an age-independent mortality can be justified by this data set.

Questions (1) and (2) can be investigated by forcing M_{t_0} to have a common value for those cohorts for which we want to test the hypotheses of a common mortality, and evaluating how well the resulting model describes the data. Question (3) can be studied by allowing a

different M_{∞} for each group of cohorts considered to have suffered the same mortality pattern, and forcing M_{t_0} to be equal to M_{∞} for all these cohorts, resulting in model

$$N_c(t_1) = N_c(t_0)e^{-M_g(t_1-t_0)} \quad (6)$$

where M_{∞} is replaced by M_g to indicate that it is no longer an asymptotic value, but rather a mortality rate which is independent of age, and exclusive to the group of cohorts to which it is associated.

Variance structure

In modelling fish abundance, it is generally reasonable to express the error in the abundance estimates as a proportion of the expected abundance. If the average size of the herring schools does not change systematically with the herring abundance, the number of schools will increase when abundance increases, and may therefore be more evenly distributed than in situations of low abundance. Under these circumstances, it seems reasonable to assume that the relative error in the abundance estimates will tend to decrease when total abundance increases.

Based on these considerations, it is assumed that the observed values, $N(t)$, are related to the values expected from the model, $E[N(t)]$, by the multiplicative error model

$$N(t) = E[N(t)]e^{\varepsilon} \quad (7)$$

Where $E[N(t)]$ is the $N(t)$ value given by (7) or (8), and ε is a random variable with

$$E[\varepsilon] = 0 \quad (8)$$

and standard error $Se(\varepsilon)$ inversely proportional to $\ln(E[N(t)])$,

$$Se(\varepsilon) = \frac{1}{\ln(E[N(t)])} \sigma \quad (9)$$

Fitting the model

The model was fitted by minimizing the sum-of-squares of the weighted residuals $\sum_i (w_i e_i)^2$,

where

$$e_i = \ln(N_i(t)+1) - \ln(E[N_i(t)]+1) \quad (10)$$

and

$$w_i = (\text{external weight})_i \ln(E[N_i(t)]+1) \quad (11)$$

Each residual is thus weighted by the inverse of its variance.

Since model (5) for $N(t)$ is intrinsically non-linear (McCullagh and Nelder 1989), a non-linear regression procedure must be used for the estimation of the parameters.

In this case, a direct-search routine, the Nelder-Mead Simplex method (Mittertreiner and Schnute 1985; Nash and Walker-Smith 1987) was used. This method was preferred to other more sophisticated methods due to the ease of its implementation and its robustness to local minima.

Hypothesis testing and evaluation of the goodness of the fit

Having defined plausible hypotheses for the patterns in mortality of young herring during the period covered by our data, it is necessary to verify which of these hypotheses agrees best with the data. Besides the most restrictive null hypothesis (that all cohorts had the same mortality), available information suggest that it may be of interest to test the alternative hypotheses that there are (a) two different mortality levels, (b) three different mortality levels or (c) nine different mortality levels (that is, each cohort experienced a different level of mortality). Since each of these hypotheses can be formulated as a different model, it is possible to test them by comparing how well the different models fit the data. The procedure of comparing the fit of the models is eased if they can be defined as a special case of a more general model (the full model).

Question (1), which cohorts could be considered to have suffered the same mortality, was investigated first. This was achieved by comparing the different groupings of the M_{t_0} parameters suggested by earlier observations. Each of these models is a special case of a model where each cohort is associated to its own M_{t_0} parameter. The full model, in this case, is model (5), with one M_{t_0} for each cohort (9 M_{t_0} -parameters).

Each candidate model is compared with the full model, using F-ratio tests in an extra-sums-of-squares analysis (Bates and Watts 1988; Draper and Smith 1981). If the model does not give a significantly worse fit than the full model, is retained for the second step of the evaluation. In the second step, the residual plots are examined to detect possible lack of fit due to inadequacy of the model specification (Bates and Watts 1988) which would not have been detected by the first test. Models which are shown to have lack of fit are rejected at this step, even if they had non-significant F-ratios. The final model selected is the simplest model of those which passed both tests.

After selecting the best grouping for the different cohorts, the hypothesis of age-independent natural mortality was tested. Model (6), in which the M_g 's were grouped according to the best grouping selected earlier, was fitted to the data, and its fit was compared to the corresponding age-dependent model. The procedure followed was the same as that used to select the best grouping of the cohorts. In this case, neither of the models is a special case of the other. They must therefore be compared to an even more general model. This model was built by expanding model (5), to consider a different M_{∞} for each group of cohorts,

$$N_c(t_1) = \begin{cases} N_c(t_0)e^{-\left[M_{\infty g}(t_1-t_0) + \frac{(M_{t_0 g} - M_{\infty g})t_0}{1-\alpha} \left(\left(\frac{t_1}{t_0}\right)^{(1-\alpha)} - 1\right)\right]} & \text{if } \alpha \neq 1 \\ N_c(t_0)e^{-\left[M_{\infty g}(t_1-t_0) + (M_{t_0 g} - M_{\infty g})t_0 \ln\left(\frac{t_1}{t_0}\right)\right]} & \text{if } \alpha = 1 \end{cases} \quad (12)$$

Determining significance of the test statistics

The use of a non-linear model with a non-additive error term whose distribution is not completely specified, prevents us from using the tabulated F-distributions to determine the significance level of the observed F-ratios. To overcome this problem, a bootstrap procedure (Efron 1982; Efron and Tibshirani 1993; Leger *et al.* 1992) was used to compute the significance of the observed F-ratios.

Both the full and the reduced model were fitted to the original data. The residuals of the fit from the full model were computed, standardized and 1000 random samples, with replacement, were taken. These randomized residuals were then combined with the values expected from the fit of the reduced model, to construct 1000 bootstrap resamples. The full and the reduced models were then refitted to each of these bootstrap resamples, and the F-ratio was recalculated for each of them. The distribution of the resulting 1000 F-ratios was taken as the distribution of the F-ratios under the null hypothesis (Hall and Wilson 1991), and used to ascertain the significance level of the observed F-ratios. The uncertainty in the "best" model was then calculated, and presented as the confidence region around the estimated survival curves. These confidence regions were also computed using a bootstrap procedure based on resampling the residuals from the fit of this "best" model. 1000 bootstrap samples were constructed, and the survival curves were estimated by fitting the model to each of them. The age interval of interest (ages 0.4 to 3 years) was divided in 500 equal intervals, and the survival at the limits of these intervals was calculated for each survival curve. The estimated survivals at each of these points were ranked, and the 2.5% and the 97.5% percentiles of these were calculated. The upper limit of the 95% confidence regions were thus defined by the set of the 97.5% percentiles of the estimated survivals at all these points, while the lower limits were built from the 2.5% percentiles.

RESULTS

The abundance-at-age values estimated for the different cohorts by fitting the full model to the acoustic abundance estimates are compared to the corresponding acoustic estimates in Figure 2. The model succeeds in reproducing the main trends in the data, and shows no lack of fit. It is therefore reasonable to base the analysis of the mortality patterns on this model.

Considering only the survival curves, i.e., removing the effect of the different recruitment levels (Figure 3), it is seen that these survival curves have a markedly clustered appearance. The curves for the 1983, 89, 90 and 91 year-classes are clearly very similar, at a high level, while those for the 1984, 85, 88 and 1993 are also relatively similar, but at the other end of the range. The estimated survival curve for the 1992 cohort lies somewhat between these two extremes, but is closer to the high-survival group.

The extra-sum-of-squares analysis (Table 1) confirms this qualitative appreciation, but indicates also that the available data do not allow us to reject the hypothesis that the difference between the survival curve estimated for the 1992 cohort and those considered as "high survival" is due to errors in the estimates of abundance.

Table 1. Extra-sum-of-squares analysis comparing the fit of different alternative models for the similarity in mortality patterns among the cohorts studied. Cohorts joined between two '/' symbols are assumed to share the same mortality pattern. d.f. - Degrees-of-freedom; ESS - Extra Sum of Squares; MES - Mean Extra Square

Model	Parameters	d.f.	ESS	MES	F-ratio	P-value
/83,84,85,88,89,90,91,92,93/	12	8	1539.06	192.38	6.949	< 0.001
/83,89,90,91,92/84,85,88,93/	13	7	81.37	11.63	0.420	0.757
/83,89,90,91/92/84,85,88,93/	14	6	67.87	11.31	0.409	0.787
/83,89,90,91,92/84,85/88/93/	16	4	12.11	3.03	0.109	0.906
/83,89,90,91/84/85/88/92/93/	17	3	1.04	0.35	0.013	0.980
Full model	20	30	830.50	27.68		

All values presented in table (except the last row, which represents the fit of the full model) refer to the extra sum-of-squares relatively to the full model. It is therefore concluded that the data do not allow us to distinguish more than two levels of survival, a very low one and a more "normal" level.

The survival curves estimated under the hypothesis of only two distinct mortality levels (Figure 4) manage to follow quite well the main patterns in the individual survival curves for each cohort, making the results of the extra-sum-of-squares analysis more intuitive.

From a stock assessment point of view, the quantity of interest is usually the survival through the juvenile period. For young herring in the Barents Sea, this may be approximated by survival to age 3 (Table 2). These estimated survivals show the same pattern which was already apparent on the survival curves plots. Survival for the whole juvenile period is estimated to be around 17% for the 1983, 89, 90 and 91 cohorts, while for the 84, 85, 88 and 93 cohorts it is estimated to be close to 0%, and 10% for the 1992 cohort. These values are again quite well approximated by the two-level model.

Table 2. Survival from age 0.4 to age 3 for the different groups of survival curves estimated. The confidence intervals were computed using a bootstrap technique.

Mortality model	Survival level	Survival to age 3 (%)	
		Point estimate	95% Confidence Interval
Two levels	High	15.8	9.4-26.8
	Low	0.3	0.0- 0.6
All Cohorts different	83	15.8	3.2-77.6
	84	0.2	0.0-1.2
	85	0.1	0.0-0.4
	88	0.4	0.0-3.5
	89	17.6	5.7-50.5
	90	17.0	9.7-28.5
	91	18.8	13.0-32.7
	92	10.4	5.2-20.1
	93	0.7	0.1-1.5

Age-independent versus age-dependent natural mortality

Since only two mortality levels could be distinguished, the test of the hypothesis of an age-independent natural mortality was performed under the two-level model. The extra sum-of-squares analysis (Table 3) clearly indicates that the hypothesis of age-independent mortality does not match the observed patterns in the data for abundance-at-age. Comparison of the

residual plots of the age-dependent and the age-independent mortality models (Figure 5) reveals that the latter shows a clear lack of fit, as it does not manage to reproduce the pattern of fast decline in abundance in the youngest ages which is a main feature of the data.

Table 3. Extra-sum-of-squares analysis comparing the fit of the age-independent and the age-dependent mortality models. d.f.-Degrees-of-freedom; ESS - Extra Sum of Squares; MES - Mean Extra Square

Model	Parameters	d.f.	ESS	MES	F-ratio	P-value
Age-independent	11	3	543.56	181.19	7.155	< 0.001
Age-dependent	13	1	0.19	0.19	0.008	0.858
Full model	14	36	911.68	25.32		

All values presented in the table (except the last row, which represents the fit of the full model) refer to the extra sum-of-squares relatively to the full model.

Assessment of precision in model fitting

The confidence regions for the estimated survival curves are presented in Figure 6 a-c). To ease the interpretation, the confidence regions for the survival curves are summarised by the 95% confidence intervals for survival between ages 0.4 and 3 years in Table 2. When estimating separate survival curves for each cohort the intervals have a very large degree of overlap. The widest confidence intervals for the high-survival cohorts even overlap with those computed for some of the low-survival cohorts. The survival curves estimated under the assumption of only two different mortality levels, on the other hand, are much better determined, and are well separated, even if the confidence intervals are still relatively wide. In both cases, the confidence regions are widest at the intermediate ages, where the degree of curvature of the curves is highest. Under both alternatives, however, survival through the juvenile phase for the 1984, 85, 88 and 93 cohorts is in the neighbourhood of 0%, while that for the other cohorts is clearly positive.

DISCUSSION

The analysis presented in this paper was based on the assumptions that the acoustic abundance estimates are unbiased estimates of the true abundance of the fish in the sea, and that the model correctly describes the true trajectory of the abundance-at-age of the different cohorts. None of these assumptions is completely satisfied, and it is necessary to evaluate the magnitude and the direction of the errors incurred in by taking them as true.

Reliability of the data

Acoustic estimates of abundance of pelagic schooling fish are subject to a number of sources of error, which decrease the precision of the estimated abundances (Simmonds *et al.* 1992). The sources of error and the reliability of the abundance estimates used in this study were discussed by Toresen and Barros (1995), and will not be dealt with further here. From the point of view of this study, the main points of interest lie in the relative degree of underestimation of the different age-groups. If the older herring are more strongly underestimated than the 0-group, then the true mortalities will be lower than those estimated here, but the age effect will be stronger. If the converse is true, then the effect will be the

opposite. As discussed by Toresen and Barros (-1995), the information available today, however, does not allow us to evaluate which, if any of these situations applies to the data used here. This possibility must, however, be taken into account when evaluating the results from this study.

For some estimates, there are nevertheless indications of more or less important errors, which may have influenced the results from this study. This is the case for the two first and the two last estimates of the 1983 year-class, which are considered to be strongly underestimated (Toresen and Barros 1995).

Another difficulty is the data for the 1989 cohort. The estimates of abundance-at-age for this cohort increase regularly after age 1, indicating a systematic error in the estimation of the abundance of this cohort. This cohort was exceptionally abundant in the fjords of Finnmark, as 0-group fish (Anon. 1994a), and its size-at-age at the older ages of the juvenile stage was much higher than the average for Barents Sea herring (I. Røttingen, I.M.R., pers. comm.). This indicates that there was most probably a significant emigration of young herring from the Finnmark fjords into the Barents Sea after age 1. To investigate the consequences of these possible errors for the conclusions of the work, we repeated the analysis by downweighting the dubious estimates in two different ways. First, we assigned a weight of 0.2 to the two first and the two last estimates for the 1983 cohort. Second, the estimates of the 1989 year-class after age 1 were downweighted in the same way. Downweighting the estimates of the 1983 year-class caused a doubling of the absolute abundance estimates of the cohort at all ages, but the estimated mortality and the inferences were relatively unchanged. The second modification led to an appreciable reduction of the estimated age-3 survival of 1989 cohort under the full model (-8%), but none of the other results were significantly affected (neither in the estimated survivals of the other cohorts nor in the inferences). It was therefore considered that none of these errors, even if they indeed existed, would significantly affect the main conclusions of the work.

The precision of the survival parameters estimated for the 1993 year-class is obviously difficult to evaluate, as only two data points are available. Yet, the observed changes in abundance are so large that the conclusion that this cohort suffered a very high mortality is difficult to impugn.

Formulation of the model

Age- and cohort effects were considered when modelling mortality. Although it can be considered that it would be more appropriate to model mortality as a function of size, rather than age, using age leads to a simpler model than if size had been considered, and we considered that it did not implicate a large loss of information, since size is also a function of age (Cushing 1974). A more relevant argument could be the one that mortality should be modelled as a year-effect, rather than a cohort-effect. In this case, however, a cohort-effect was considered a more adequate formulation. Younger and smaller fish are likely to be more affected by these changes in the environment than the larger herring, and the one-year interval between consecutive cohorts makes each cohort well individualised, while defining the changes as year-effects would imply setting an arbitrary cut-point between years.

Evaluation of the results

The results obtained in this study show that the statistical modelling approach may give quite useful contributions to the study of inter-cohort variability in survival of juvenile Norwegian spring-spawning herring. This variability in survival is very high, and mortality rates during this life-stage are strongly age-dependent. Both null hypotheses which were put forward at the start of the study can therefore be rejected with a high degree of confidence.

The time series investigated are quite short, and cover only one period in which the herring stock is increasing (a "one-way trip", in the terminology of Hilborn and Walters 1992). One must therefore be careful when extrapolating the conclusions of this work. Nevertheless, some aspects revealed by this study may have a general relevance, and are worth discussing.

The sheer magnitude of the differences in survival among the cohorts investigated is overwhelming. The mortality experienced by the cohorts in the "high-mortality group" was so high that they were practically extinct by the end of the juvenile period. Given this large difference, and that only two levels of mortality could be conclusively demonstrated, the dynamics of the juvenile herring in the period investigated can be described as an "all or nothing" situation. Cohorts can accordingly be classified as either "success" or "failure", setting another dimension to the evaluation of the effects of variable mortality in recruitment. In this perspective, the high proportion of cohorts which can be classified as "failures" (4/9, or practically 50%) must be considered as a strong evidence that year-class strength of this stock can (and most probably frequently is) determined by variable mortality at the juvenile stage. This study is thus a test of Hjort's (1914) hypothesis that year-class strength is determined in the larval stage. The results obtained indicate that this hypothesis must be rejected for the Norwegian spring-spawning herring stock. Most other studies addressing this question could not reject Hjort's hypothesis (Myers and Cadigan 1993). This may be due to the fact that for very few stocks is there data series of the quality and length of the one used in this study, especially data including the youngest juvenile stages, where large variability in mortality is most likely to occur.

The age-dependent effect in mortality was estimated to be very strong. This implies that most of the juvenile mortality occurs during the first year of life, and that older herring (2-group and late 1-group) are much less susceptible to these variations in mortality. The existence of a strong size-dependent mechanism conditioning mortality is therefore strongly suggested by this study. Studies of this aspect would probably shed some light on the actual processes mediating mortality in this stock (which might be generalizable to other stocks), and would probably be worth investigating deeper.

In a management perspective, the main application of studies on the mortality of juveniles lies in improving the forecasts of recruitment. This requires the capacity to predict the changes in juvenile survival. The procedure developed here can be used to describe the patterns in juvenile herring mortality and to test hypotheses about their variations, once these have occurred. It can also be used to forecast recruitment, once at least one estimate of abundance and the mortality level expected for the given cohort are available. It does not provide a means to predict this mortality, however, and consequently it cannot be directly used for prediction.

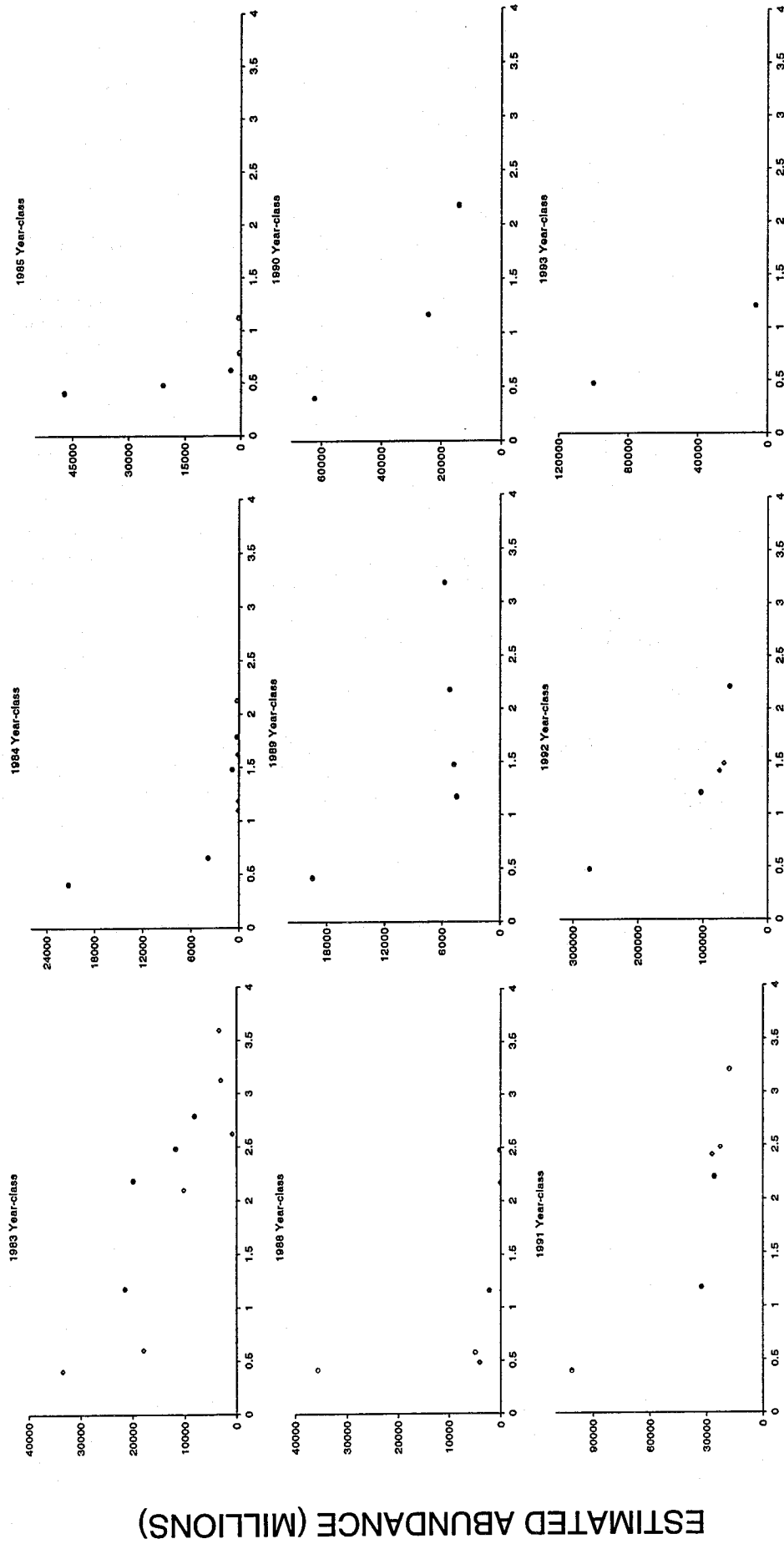
Hamre (1988 1994) has suggested that the variations in mortality of young herring in the Barents Sea are due to variable predation pressure by Northeast Arctic cod, and studies of cod stomach contents (e.g. Mehl 1989) seem to support this hypothesis. For applying this in assessment work, it is necessary to develop a suitable measure of the cod's predation pressure

on the young herring, and to quantify the relationship between this measure and herring mortality. It is also required to demonstrate convincingly that the observed variations in herring mortality can be explained by corresponding variations in the cod predation pressure, and that the latter can be used to effectively predict the changes in herring mortality. This will require careful consideration of the species interactions in the Barents Sea, and stresses the relevance of the current work aimed at expanding the multispecies modelling efforts for the area (e.g. Tjelmeland and Bogstad 1993) to include the juvenile herring, which is getting increasing importance in this ecosystem (Hamre 1994; Anon. 1994b).

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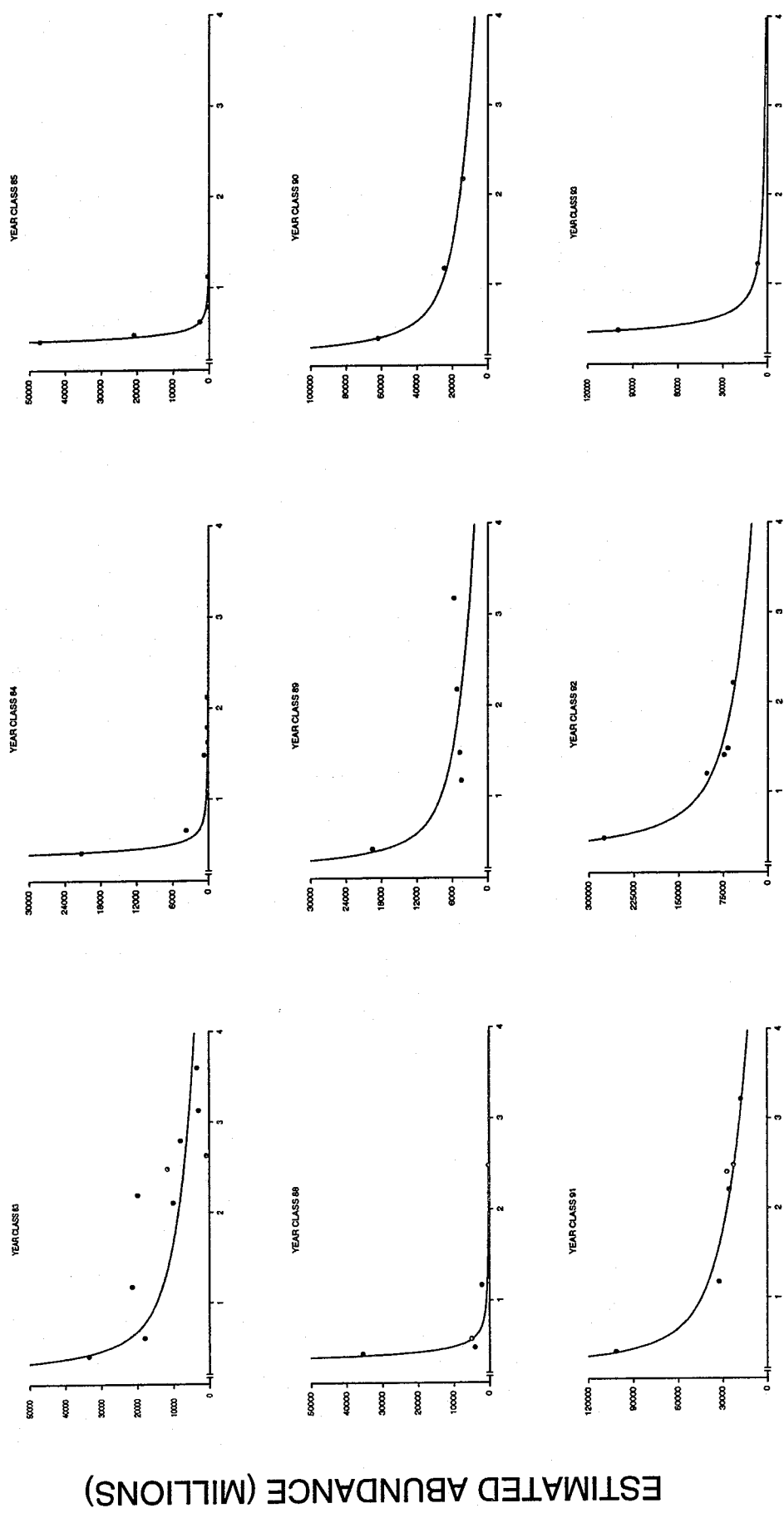
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AGE (YEARS)

Figure 1. Acoustic abundance estimates available for the 1983-1985 and 1988-1993 year-classes. Estimates of "normal" quality; Estimates of dubious quality



AGE (YEARS)

Figure 2. Abundance-at-age predicted from the full model and corresponding acoustic estimates, for juvenile stage of cohorts 1983-1993 in the Barents Sea.

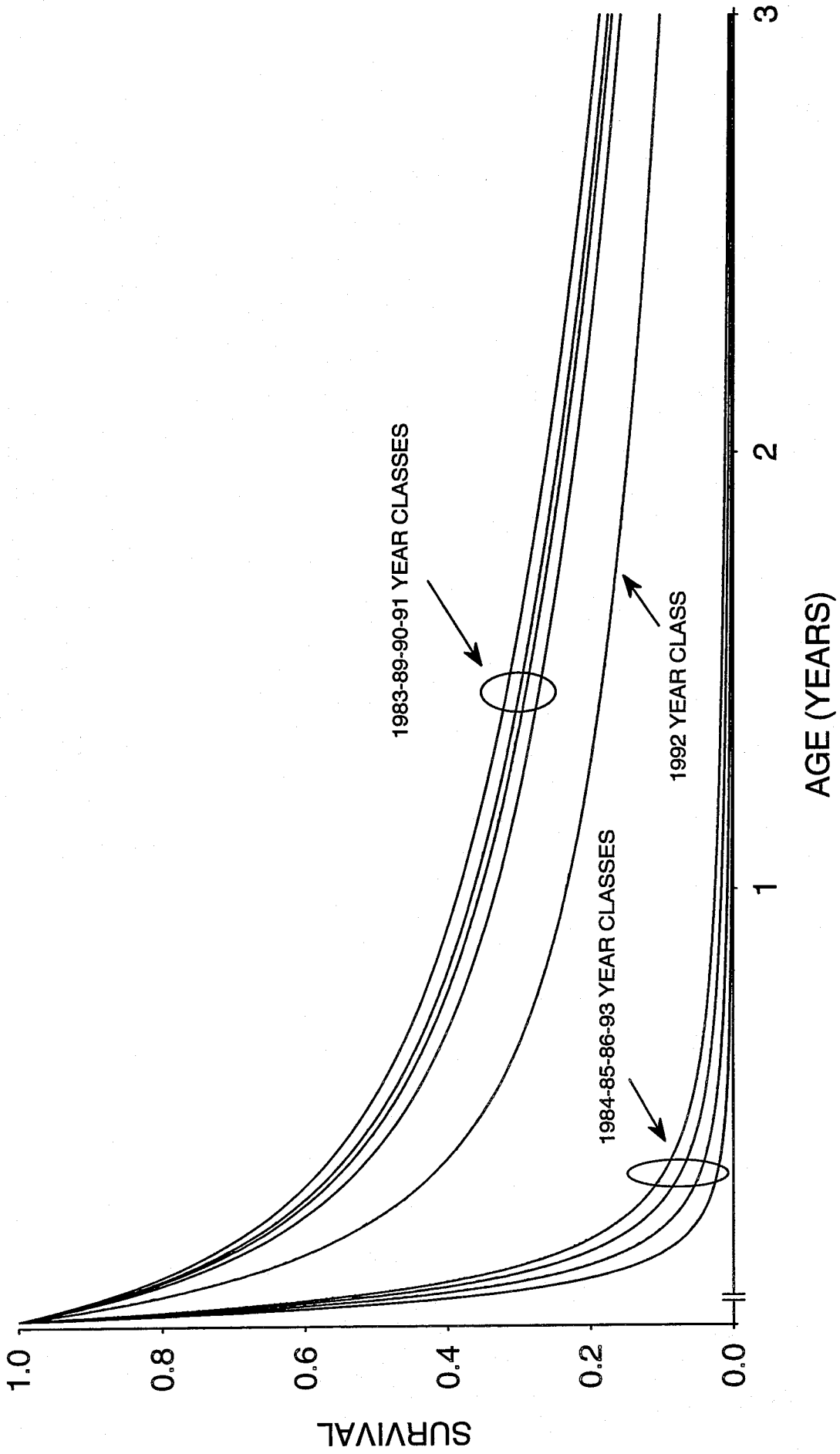


Figure 3. Survival curves estimated under the full model.

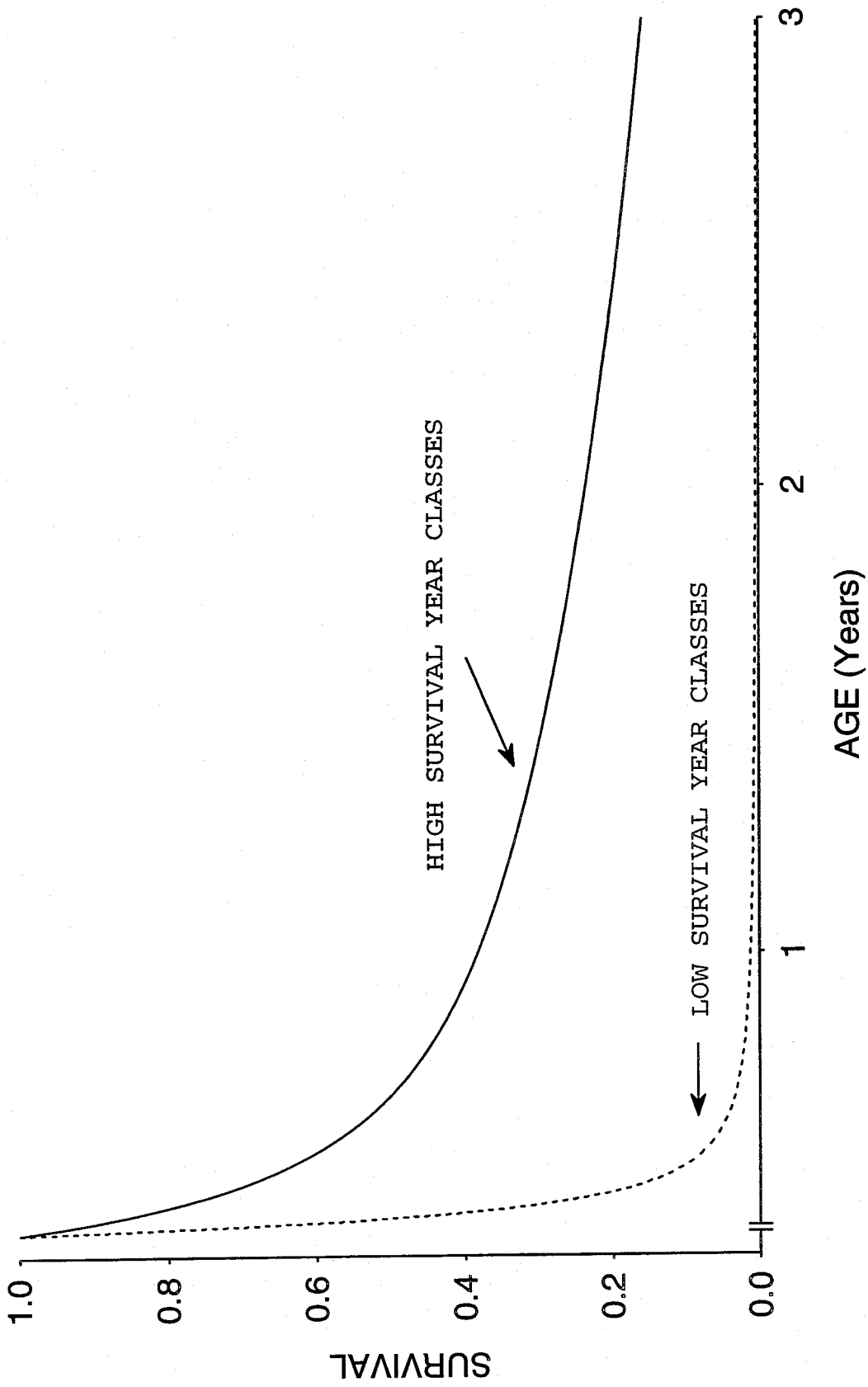
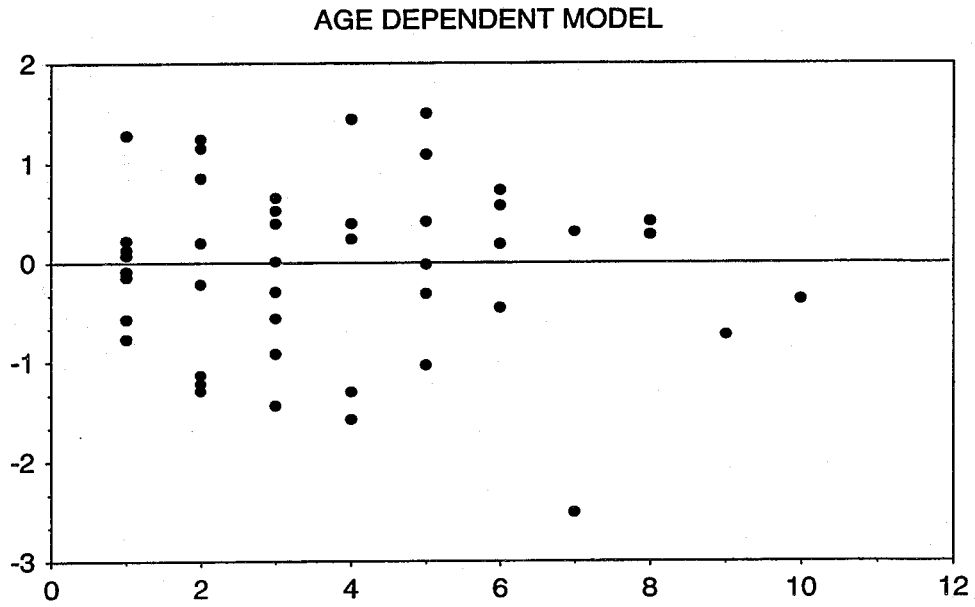
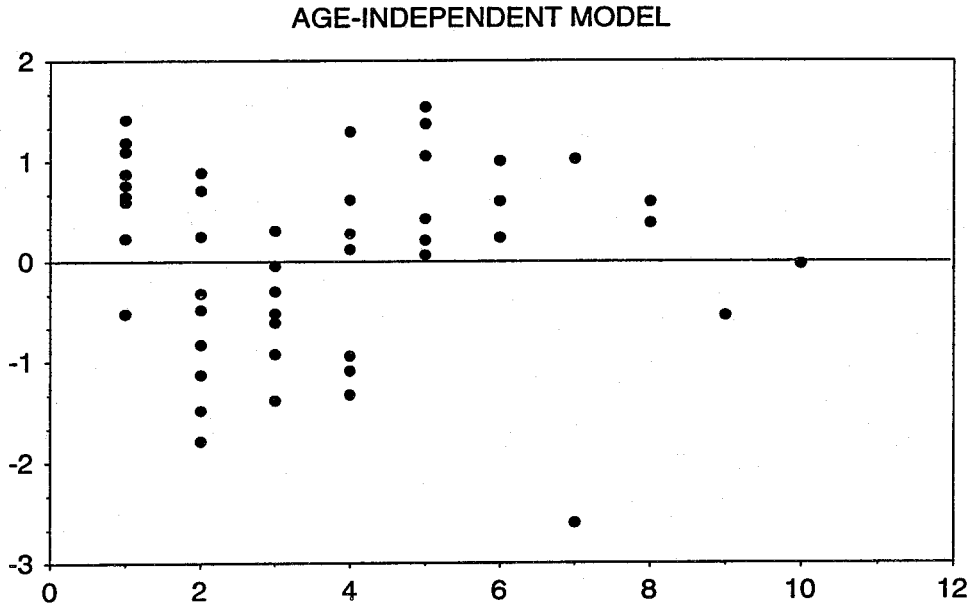


Figure 4 Survival curves estimated under the two-mortality levels model. 259

STANDARDIZED RESIDUALS



ORDER OF OBSERVATION

Figure 5. Comparison of residual plots for fit of age-independent and age-dependent mortality models.

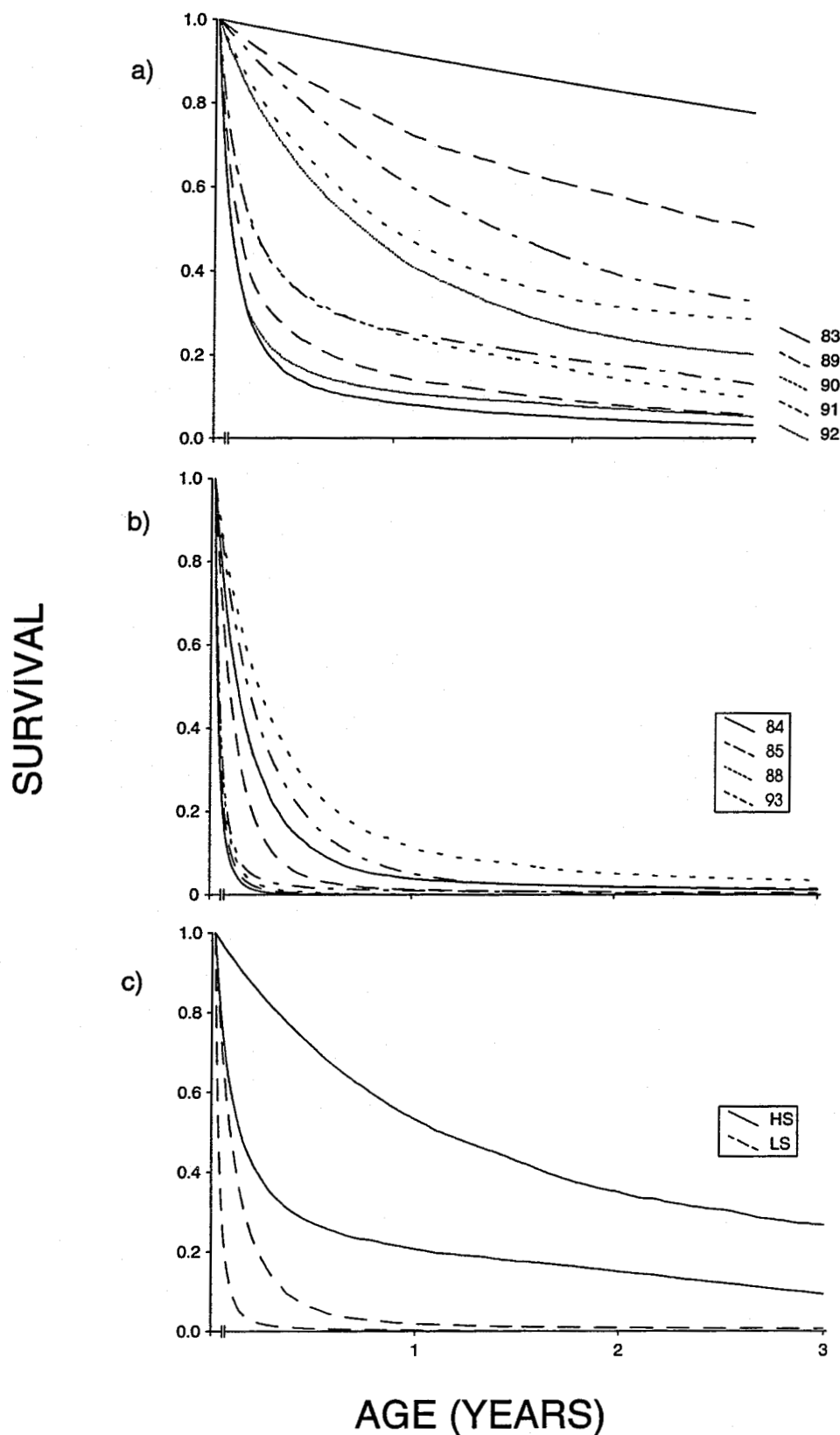


Figure 6. Confidence regions for survival-at-age during the juvenile stage of herring in the Barents Sea. a) Full model, high-survival cohorts. b) Full model, low-survival cohorts. c) Reduced model, high-and low-survival cohorts.